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Research Article

First insights in terrestrial mammals monitoring in the Candelaria and Machay Reserves in the Ecuadorian Tropical Andes

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Abstract

Habitat disturbance leads to biodiversity decline and modifications in the landscape structure and composition, affecting both dispersal movements and ecological processes at different temporal and spatial scales. The Ecuadorian Tropical Andes harbour suitable habitats for the distribution of a wide variety of species; however, there is a lack of studies focused on mammal diversity and its association with the habitat attributes in the central-eastern slopes. Here, we reported the diversity of terrestrial mammals recorded between 2019 and 2021 in a camera-trap monitoring study in the Candelaria and Machay reserves

in the upper basin of the Pastaza River, Ecuador. We performed site-occupancy probability analysis to assess the influence of spatial variables in the species' occurrence and also, based on natural marks, we reported preliminary findings in Andean bear individual identification. We detected 22 species of terrestrial mammals. Alpha diversity was similar between reserves with slightly higher species richness in Machay. Evenness indices showed unequal species distribution, with the Andean bear and domestic dogs exhibiting greater dominance. In addition, species composition was dissimilar between reserves, where the species turnover mostly explained the beta diversity. We observed that Andean bear and puma detections increased according to the natural vegetation cover. Conversely, domestic dogs were frequently detected in cells with an increasing proportion of pastures and crops. Additionally, we identified 26 Andean bears and six individuals recaptured during our study. Our results caution about the disturbance derived from human activities since we recorded unprecedented detections of domestic dogs in wild habitats. Nonetheless, it highlights the importance of private conservation areas (e.g. Candelaria, Machay and others) for supporting the occurrence and dispersal of terrestrial mammal species between larger areas in the upper basin of the Pastaza River.

Keywords

ecological corridors, CELS, landscape ecology, mammal diversity, photo identification

Introduction

The main causes for the global biodiversity decline include forest clearing, natural resources overexploitation, habitat change, invasive alien species, hunting, climate change, fires and pollution (Pereira et al. 2012, Newbold et al. 2015). Accordingly, land-use change modifies the spatial structure and composition of landscapes and decreases habitat connectivity by reducing suitable habitat patches for wildlife dispersal within the landscape, which ultimately impacts the species' population viability (Metzger and Décamps 1997, Goodwin and Fahrig 2002, Beier et al. 2011, Lawler et al. 2013, Leonard et al. 2017, Marrotte et al. 2017). However, its effects vary according to the matrix features, the target species and scale of analysis (Krausman 1999, Zeller et al. 2012, Marrotte et al. 2017). For instance, species with broad habitat range take advantage of the interpatch distances and use small area patches as stepping-stones to travel between core areas, whereas species with small habitat range benefit from the small area patches' contribution to intrapatch connectivity (Goodwin and Fahrig 2002, Herrera et al. 2017). Additionally, habitat loss and fragmentation impact differentially, the former being more negative for connectivity due to its effects on the habitat amount and patch isolation (Goodwin and Fahrig 2002). Similarly, road development is the primary cause of habitat fragmentation and constitutes a barrier to the movement of several species, preventing their dispersal ability to travel and access resources within the landscape (Laurance et al. 2009, Seidler et al. 2015, Beyer et al. 2016, Medrano-Vizcaíno and Espinosa 2021). Thus, increasing habitat connectivity networks (i.e. the availability of routes to support the species' physiological, behavioural and dispersal requirements within the landscape) is a common

strategy to improve wildlife conservation planning (Beier and Noss 1998, Belote et al. 2016, Albert et al. 2017).

The tropical Andes are biodiversity hotspots critical for the provision of ecosystem services (Myers et al. 2000, Gaglio et al. 2017). Nonetheless, poor land management and intensive land-use change in anthropogenic landscapes impacts on the species survival rate, either by reducing the habitat availability, species movement capacity or due to the increase in the mortality risk of species occurring close to human features (Nielsen et al. 2010, Cavelier et al. 2011, Fletcher et al. 2019). The foothills and eastern slopes of Ecuador are characterised by rugged topography and dense vegetation that creates montane cloud forests and paramos (Simpson 1975, Sánchez et al. 2018). These ecosystems, typical of the tropical Andes, provide suitable habitats for the distribution of a wide variety of species, many of them with restricted distributions and endemic to the area (Gradstein et al. 2004, Jost and Shepard 2017, Reyes-Puig et al. 2022), but also large and medium-sized mammal species with much larger territory requirements due to their nature and dispersal ability. In this context, studies focused on mammal monitoring on the central-eastern slopes of Ecuador are scarce, as well as those attempting to address the variables affecting the species' site occupancy. Similarly, updated richness and diversity analyses of medium- and large-sized terrestrial mammals through standardised monitoring is not yet available.

In this paper, we present the first results of a two-year pilot camera-trap monitoring study of medium- and large-sized mammals in which we identified the richness and diversity of species of two reserves located in the east-central Andes of Ecuador (Machay and Candelaria), in the upper basin of the Pastaza River. In addition, we estimated the occupancy and detection probability of this group and its association with spatial variables and finally we took advantage of the methodology to recognise unique individuals of spectacled bears that allow us to warn about the importance of the region for habitat connectivity, conservation and management of landscape species.

Material and methods

Study area

We conducted the study in the eastern slopes of the Andes in Ecuador, in the Cerro Candelaria and Machay Reserves of the Fundación Ecominga (Fig. 1). The study area comprehends 74 km2 (defined as the minimum convex polygon around the camera stations). It is part of the so-called Llanganates – Sangay Ecological corridor (hereafter CELS) which encompasses public and private lands with important remnants of natural habitats between two National Parks, Llanganates to the north and Sangay to the south (Ríos-Alvear and Reyes-Puig 2015). CELS possesses geological and climatic characteristics which have favoured high levels of endemism and species diversification within a narrow territory (Jost 2004). Its strategic location is essential for promoting habitat connectivity (Lessmann et al. 2014, Ríos-Alvear and Reyes-Puig 2015, Cuesta et al. 2017), linking protected areas and well-preserved habitat remnants critical for the

conservation of species with different habitat requirements (Reyes Puig and Ríos Alvear 2013, Ríos Alvear and Reyes Puig 2013, Lopez de Vargas Machuca 2014, Reyes-Puig et al. 2015). The study area includes cloud forests and paramos ranging from 1527 to 3710 m in elevation devoted to strict conservation management, embedded in a human-dominated landscape with different degrees of disturbance. The precipitation regime extends from April to July and October to December, with rains up to 5000 mm (Crespo et al. 2011, Ilbay-Yupa et al. 2021). The average annual temperature ranges between 12.3°C and 27.6°C (INAMHI, National Institute of Meteorology and Hydrology- Ecuador 2022).
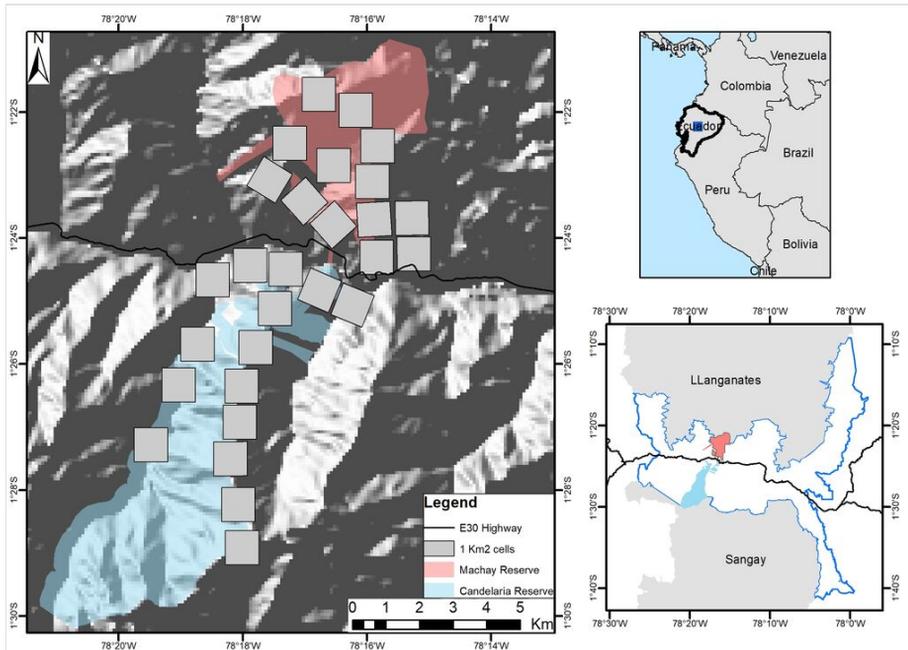
Figure 1. doi

Study area. Large map shows the Machay Reserve in the north and the Candelaria Reserve in the south. Grey squares represent the sampling areas. The bottom right map shows the Llanganates and Sangay National Parks and the study area within the CELS (blue line).

Camera trap survey

We conducted a camera-trap survey consisting of four sampling campaigns, from late 2019 to 2021. We defined 15 cells of 1 km^2 at each Reserve. Each sampling cell was surveyed twice a year with one camera trap active during the dry and rainy seasons. Effective sampling days varied from 12 - 65 due to the camera's performance and the lockdown and mobility restrictions caused by the COVID-19 pandemic outbreak (Table 1). Sampling cells were selected according to accessibility. We placed one camera per cell at 1 km apart from each other, following wildlife trails to improve species detectability, particularly in areas that potentially favour connectivity between the reserves. Cameras were deployed in the same spot during the entire study. We set a minimum 60-minute interval between each detection

(video or photo) as an independent record of the same species (Rovero and Marshall 2009). We defined this range to prevent the bias caused by overcounting the detected species. We used Bushnell Trophy Cam HD Aggressor (model 119875). Cameras were active 24 hours a day, set at normal sensitivity in hybrid mode to record three pictures and one video of 30 seconds per detection event. No attractants were used during sampling.

Table 1.

Sampling effort.

Sampling campaign	Date		Active cameras		Effective sampling days Mean (± SD)	
	Start	End	Cerro Candelaria	Machay	Cerro Candelaria	Machay
F1	December 2019	April 2020	12	9	58.66 (± 37.7)	58.3 (± 60)
F2	October 2020	December 2020	14	12	49 (± 17.4)	36.2 (± 25.2)
F3	April 2021	July 2021	9	9	34.1 (± 34.8)	36.6 (± 33.7)
F4	August 2021	October 2021	14	11	45.87(± 29)	46.1(± 31.8)

Data analysis

Species relative abundance

We computed the species relative abundance, based on the average number of independent camera trap records during 100 trap-nights in each Reserve during our study (Rovero and Marshall 2009).

Diversity analysis

We estimated alpha and beta diversity for each Reserve. Diversity analyses were conducted following the Hill numbers approach (i.e. the effective number of species) (Jost 2006, Chao et al. 2014). The first four Hill numbers were used: namely H0 as species richness, H1 derived from the Shannon-Wiener exponential index, H2 derived from Simpson's inverse index and H3 from the Berger-Parker index for species dominance. However, we also included the standard indices from which Hill numbers are derived for comparison. For dominance we applied the Berger-Parker index (d) and for evenness, we used Simpson's index I, Pielou's index (J) and Smith & Wilson's index (Smith and Wilson 1996). In order to compare whether there were significant differences between the alpha diversity of the two localities, we performed a Dunn's post hoc test. For beta diversity, we took into account the beta partitioning approach, considering the contribution to differences in beta diversity due to species replacement and richness difference (Carvalho et al. 2012, Cardoso et al. 2014). We used Jaccard's similarity index to assess this pattern. We used

interpolation and extrapolation curves to estimate diversity (Chao et al. 2014). For extrapolation, we calculated non-parametric estimators, Chao1 which provide a lower bound on the true diversity of the community, based on abundance data, Chao2 that allows correct sample size using incidence data and Jackknife estimators that reduce the bias for observed richness (Gotelli and Chao 2013). The model used for diversity estimators is derived from sample-based data (incidence data). Here, we did not consider the individuals (abundance data), but the sampling units, which in our case, are camera traps. In this regard, presences are treated as incidences and absences as non-detections for each species within each sampling unit. An incidence matrix is generated and the sum of the rows is used to obtain the incidence-based frequency of a species. Hill numbers are estimated, based on the Bernoulli distribution (Chao et al. 2014b). We performed our analyses with the packages "vegan" (Oksanen et al. 2007), "BAT" (Cardoso et al. 2015), "iNEXT" (Hsieh et al. 2016) and "dunn.test" (Dinno and Dinno 2017) in R.

Site-occupancy modelling

We modelled the site-occupancy probability, defined as the proportion of habitat occupied by a particular species under the assumptions of closed population within, but not between seasons, sampling independence and equal probability of occupancy and detection across sampling sites and surveys (MacKenzie et al. 2018). Occupancy models take into account imperfect detection, preventing naïve estimations derived from not detecting the species even when it is present at a site, but also assess the effects of variables as triggers for occupancy and detection probabilities (MacKenzie et al. 2002). We performed multi-season occupancy models to assess the effects of habitat covariates in the occurrence of the terrestrial mammal species in the study area, taking into account the effects of rain seasonality and the presence of domestic dogs as factors leading to changes in occupancy patterns between seasons. We hypothesised the effects of vegetation coverage, protected areas, human accessibility and topography as site attributes affecting occupancy, whereas sampling effort, topography and presence of dogs as sampling variables that influence the probability of detection of wildlife species (MacKenzie and Bailey 2004) (Table 2). We compiled site covariates from Ecuador's National Thematic Cartography repository and a satellite image classification of a Sentinel 2 image. The site variables were calculated from the location of the camera traps, except the vegetation cover, which corresponds to the average proportion at 1 km^2 and 250 m of buffer for each camera. Sampling covariates and the presence of dogs were collected from the camera trap records. We estimated site-occupancy probability with the package "unmarked" (Fiske and Chandler 2011).

We assessed the spatial arrangement of detections according to the spatial features within the study area to identify potential characteristics influencing the occurrence of the modelled species. We applied the Wilcoxon-Mann-Whitney test to assess the differences between detections and non-detections within the study area and summarised the results through the "ggstatsplot" R package (Patil 2021).

Table 2.

Hypothesis for site-occupancy probability estimates. ψ (Occupancy probability) and p (Detection probability) ɣ (Colonisation probability), ε (extinction probability). For j = sites, i = species and K_j = surveys at each site.

Variable	Model	Description	Conceptual model
Vegetation (Veg)	$logit\,(\psi_i) = \beta_0 + mean\ Veg_j$	Proportion of vegetation within the 1 km² sampling cell and at 250 m buffer surrounding each camera trap. We defined three classes: 1. Natural vegetation 2. Pastures and crops 3. Areas without vegetation.	1. The occupancy of wildlife species increases at high proportions of natural vegetation. 2. The occupancy of wildlife species increases at low proportions of pastures and crops. 3. The occupancy increases at low proportions of areas without vegetation.
Distance to Protected Areas (PAdist)	$logit\,(\psi_i) = \beta_0 + PAdist_j$	The nearest Euclidean distance from the camera trap to the border of the protected areas.	The occupancy of wildlife species increases closer to the protected areas.
Distance to creeks (Cdist)	$logit\,(\psi_i) = \beta_0 + C_j$	The nearest Euclidean distance from the camera trap to creeks.	The occupancy of wildlife species increases closer to creeks as they provide natural corridors for dispersal.
Distance to roads (Rdist)	$logit\,(\psi_i) = \beta_0 + Rdist_j$	The nearest Euclidean distance from the camera trap to roads.	The occupancy of wildlife species increases at a high distance from roads.
Human accessibility (Acces)	$logit\,(\psi_i) = \beta_0 + Acces_j$	Probability of human access to a pixel as a function of the existence of roads, vicinity to human settlements and navigable rivers (Ríos-Franco et al. 2013).	The occupancy probability increases at a low probability of human accessibility.
Rugosity (Rugos)	$logit\,(\psi_i) = \beta_0 + Rugos_j$ $logit\,(\psi_i) = \alpha_0 + Rugos_j$	Raster obtained from the MODIS satellite computed as a function of elevation, shape and topographic slope.	The occupancy probability increases at high levels of rugosity as a proxy of less disturbed areas. The detection probability decreases as rugosity increases.
Forest loss (Floss)	$logit\,(\psi_i) = \beta_0 + Floss_j$	Rate of tree canopy removal from 2000 - 2018 (RAISG 2020).	The occupancy probability is higher in areas with low rates of forest loss.
Forest gain (Fgain)	$logit\,(\psi_i) = \beta_0 + Fgain_j$	The establishment of tree canopy from a non-forest state from 2000 – 2012 (Hansen et al. 2013).	The occupancy probability increases in areas with high rates of forest gain.
Ecological integrity index (EII)	$logit\,(\psi_i) = \beta_0 + EII_j$	Forest condition determined by the degree of human pressures and loss of habitat connectivity (Grantham et al. 2020)	The occupancy probability increases in areas with high ecological integrity.
Rain seasonality (Rain)	$logit\,(\chi_i) = \beta_0 + Rain_j$ $logit\,(\varepsilon_i) = \beta_0 + Rain_j$	Indicator variable to reflect the rain regime during the sampling campaign (Crespo et al. 2011, Ilbay-Yupa et al. 2021)	The occupancy changes between sampling seasons according to the rain regime.

Variable	Model	Description	Conceptual model
Occurrence of domestic dogs (Dogs)	*logit* $(\psi_i)= \beta_0$ + Dogs$_j$ *logit* $(\psi_i)= \alpha_0$ + Dogs$_j$ *logit* $(\gamma_i)= \beta_0$+ Dogs$_j$ *logit* $(\varepsilon_i)= \beta_0$ + Dogs$_j$	Occurrence of domestic dogs recorded by the camera traps during the sampling campaign	The occupancy and detection probabilities are higher in areas where domestic dogs are absent. The occurrence of domestic dogs leads to changes in occupancy between seasons.
Sampling effort (eff)	*logit* $(z_i \, p) = \alpha_0$ + eff K$_j$)	Effective sampling days of the camera traps	Detection probability increases as more sampling effort devoted.

Photo-identification

We performed a photo identification only for Andean bears, based on their facial marks (García-Rangel 2012, Horn et al. 2014) (Fig. 2). We selected the camera-trap records containing Andean bears with facial scenes subject for identification (i.e. clearly visible facial marks). We classified the pictures according to the scene captured (e.g. right-side face, left-side face, front scene, throat) and compared them according to the natural marks photographed. We performed three independent reviews of the photographs between sampling campaigns. In addition, due to the broad home range of the species (Rodriguez et al. 2021), we identified the individuals recaptured between sample campaigns only. We excluded the poor-resolution Andean bear pictures to prevent mistakes and ambiguities in the identification.

Figure 2. doi

Colouring pattern used for individual identification of Andean bears. Picture by Santiago Recalde.

Results

We documented 284 independent camera-trap records of medium and large-size terrestrial mammals in 2814 sampling days at the Candelaria Reserve and 218 records in 2658 sampling days at the Machay Reserve. Species' relative abundance ranged from 0.03 to 3.13 camera records per 100 sampling days (Table 3).

Table 3.

Photographic rate of the species recorded in the camera trapping monitoring at the Candelaria and Machay Reserves during 2019 – 2021. We compared our findings with a previous study in the Llanganates National Park.

			Relative abundance (± 90% CI)		
			Our study		Palacios et al. (2018)
Order	**Family**	**Species**	**Candelaria**	**Machay**	
Artiodactyla	Cervidae	*Mazama rufina*	0.33 (0.38)	0.62 (0.95)	0.82 (0.81)
		Pudu mephistophiles		0.16 (0.25)	0.69 (0.70)
	Tayassuidae	*Tayassu pecari*	0.04 (0.09)		
Didelphimorphia	Didelphidae	*Didelphis albiventris*	0.3 (0.7)	0.1 (0.23)	
		Didelphis pernigra	0.15 (0.28)	0.46 (0.4)	0.39 (0.35)
Carnivora	Canidae	*Canis familiaris*	1.42 (1.61)	0.76 (0.6)	
	Felidae	*Leopardus tigrinus*	0.76 (0.77)	0.68 (0.43)	0.30 (0.26)
		Puma concolor	0.8 (0.43)	0.99 (1.2)	0.65 (0.35)
	Mustelidae	*Eira barbara*	0.33 (0.3)	0.37 (0.33)	
		Mustela frenata	0.03 (0.08)	0.17 (0.41)	
	Procyonidae	*Nasua nasua*	0.27 (0.27)	0.74 (0.26)	
		Nasua olivacea	0.24 (0.46)	0.07 (0.1)	0.26 (0.22)
	Ursidae	*Tremarctos ornatus*	3.13 (1.58)	2.32 (3.24)	0.86 (0.48)
Perissodactyla	Tapiridae	*Tapirus pinchaque*		0.4 (0.68)	1.64 (1.22)
Pilosa	Myrmecophagidae	*Tamandua tetradactyla*	0.3 (0.36)		
Primates	Cebidae	*Cebus yuracus*	0.03 (0.06)		
Rodentia	Cuniculidae	*Cuniculus paca*		0.04 (0.09)	
		Cuniculus taczanowskii		0.1 (0.25)	0.34 (0.28)
	Dasyproctidae	*Dasyprocta fuliginosa*	0.67 (0.71)	0.4 (0.56)	
	Leporidae	*Sylvilagus andinus*		0.07 (0.16)	
	Sciuridae	*Microsciurus flaviventer*	0.41 (0.97)	0.03 (0.08)	
		Syntheosciurus granatensis	0.05 (0.06)	0.44 (0.88)	

Diversity analysis

We detected a total of 22 species of terrestrial mammals in 502 independent camera-trap records. We recorded 17 species at the Candelaria and 19 at the Machay Reserve. Alpha diversity appears to be similar between Reserves with a slight increase in the number of species in Machay (Table 3). H3 showed some degree of dominant species in the two localities (Table 4). This was corroborated by the total number of independent records detected during sampling campaigns (Fig. 3), where the Andean bear and domestic dogs exhibited the highest number of records. The Pieleu, Simpson and Smith & Wilson Evenness indices showed, as a general trend, that the species relative abundances are not equally distributed, with some degree of variation between sampling campaigns (Table 4). We identified similar values for the Hill numbers in both localities (Table 4). Jaccard Similarity index (β_{total} = 0.64) suggested that the species composition is dissimilar, with some species recorded either in Candelaria or Machay (Suppl. material 1) (Table 3, Fig. 3 B). Most of the beta diversity was explained by beta richness difference rather than by beta replacement (β_{rep} = 0.17, β_{rich} = 0.47).

The estimated diversity for Candelaria and Machay communities through rarefaction and extrapolation curves indicated the same trend showed by alpha diversity, identifying Machay as the more diverse locality (Fig. 4, Table 4). The extrapolation to reach the asymptote in species diversity within localities can be reached at 20 sampling units (Fig. 4 A). The completeness or sample coverage was high in both locations, reaching the asymptote already at rarefaction (Fig. 4B). First-order Jackknife and Chao estimators were congruent in their estimates, identifying the potential addition of at least two more species in Candelaria and Machay; however, Machay would increase the larger number of species (Table 5).

Table 4.

Summary of medium- and large-size mammal's diversity indices and Hill numbers. H0: species richness, H1: Shannon-Wiener exponential, H2: the reciprocal of Simpson and H3: Berger-Parker index, J: Pielou's index, E: Simpson's index.

Index	Candelaria					Machay				
	F1	F2	F3	F4	Total	F1	F2	F3	F4	Total
H0 (S)	13	12	7	12	17	13	11	14	12	19
H1 (exp H')	8.62	9.23	3.65	4.76	10.15	6.34	6.04	10.69	10.31	11.31
H2 (1/D))	6.12	7.76	2.47	2.86	7.28	3.91	3.88	8.69	9.29	8.40
H3 (d)	4.85	6.93	2.09	2.37	5.90	3.14	3.15	7.63	7.61	6.90
J	0.83	0.89	0.67	0.63	0.82	0.72	0.74	0.89	0.94	0.82
E	0.47	0.65	0.35	0.24	0.43	0.30	0.35	0.62	0.77	0.44
Smith & Wilson index	0.60	0.65	0.76	0.42	0.40	0.64	0.61	0.69	0.71	0.40
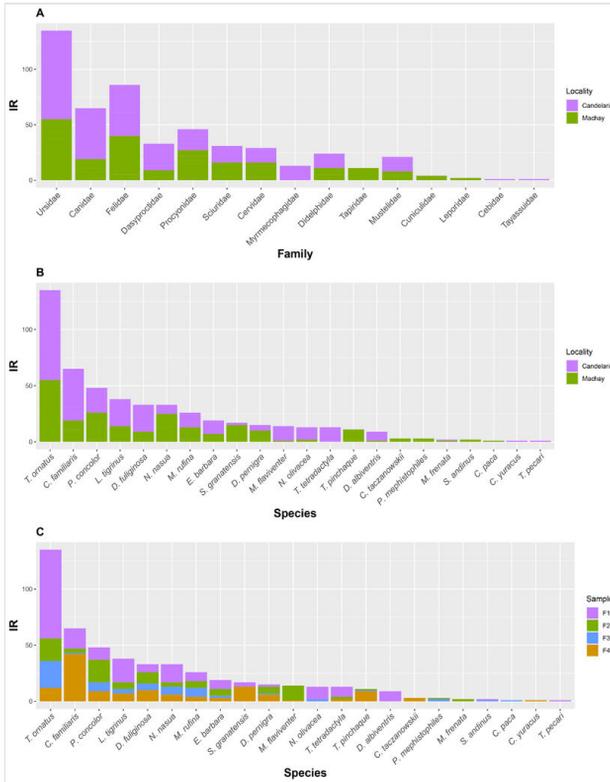
Figure 3. [doi]

Documented independent records for medium and large-size terrestrial mammal species. **A** By family; **B** By species; **C** By sampling campaign.

Table 5.

Diversity estimators of medium- and large-size mammals in the Candelaria and Machay Reserves. Obs: Observed species richness, S1: singletones, S2: doubletones, Jack1ab: first order Jackknife, Jack2ab: second-order Jackknife, Chao 1: Chao estimator based on abundance and their bias-corrected complements (Jack1abp, Jack2abp, Chao1P).

		Obs	S1	S2	Jack1ab	Jack1abp	Jack2ab	Jack2abp	Chao1	Chao1P
Candelaria	**F1**	13	2	0	15	15.36	17	17.4	14	14.33
	F2	12	2	1	14	14.39	15	15.42	12.5	12.85
	F3	7	3	1	10	11.84	12	14.2	8.5	10.06
	F4	12	7	1	19	25.47	25	33.51	22.5	30.16
Machay	**F1**	13	3	3	16	16.85	16	16.85	13.75	14.48
	F2	11	7	1	18	25.29	24	33.72	21.5	30.21
	F3	14	7	2	21	26.25	26	32.5	21	26.25
	F4	12	1	1	13	13.09	13	13.09	12	12.08
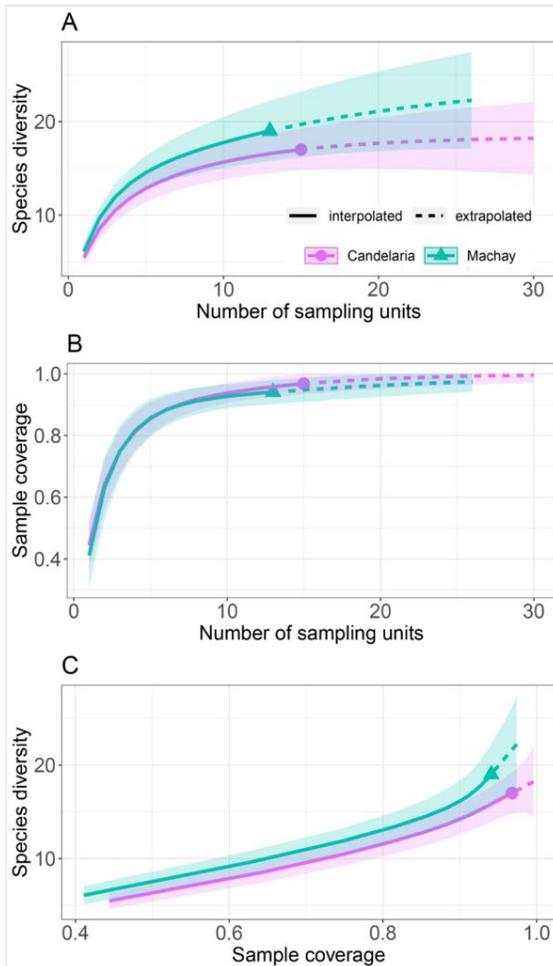
Figure 4. doi

Rarefaction (solid lines) and extrapolation (dashed lines) curves for the medium- and large-size mammal communities in the Candelaria and Machay Reserves. **A** Estimated species diversity according to the sampling units; **B** Estimated sample coverage according to the sampling units; **C** Estimated species diversity according to the sample coverage.

Site-occupancy modelling

We estimated the occupancy probability for the Andean bear, puma, oncilla and domestic dogs since they exhibited the highest number of detections recorded during the study (Fig. 3C). Occupancy probability was higher for the Andean bear and puma ($\Psi = 0.6$ and $\Psi = 0.4$, respectively), while detection probability was higher for the Andean bear and domestic dogs ($p = 0.27$ and $p = 0.22$, respectively) (Table 6). However, we did not find any significant effect of the candidate variables in the occupancy probability for the species modelled (Suppl. material 2).

Table 6.

Average occupancy (ψ) and detection probabilities (p), based on the null models (ψ(.)p(.)) for the Andean bear, puma, oncilla and dogs in the Candelaria and Machay Reserves.

	Delta AIC	ψ (± SE)	p (± SE)
Andean bear	4.59	0.6 (0.1)	0.27 (0.06)
Puma	3.34	0.4 (0.1)	0.17 (0.08)
Oncilla	0	0.33 (0.1)	0.1 (0.08)
Domestic dogs	0	0.2 (0.1)	0.22 (0.2)

According to the camera traps placement, we observed that 78%, 93% and 74% of Andean bear detections were significantly more frequent in cells with a high proportion of natural vegetation, at very low levels of vegetation absence at a 1 km^2 scale and in areas with low levels of rugosity, respectively (rugosity index range = 1.05-1.3) (Fig. 5). Pumas were recorded significantly more frequently in cells where the proportion of natural vegetation was high both at 1 km^2 (78% of detections) and at the buffer scale (87% of detections), but also when the proportion of vegetation absence was low at both scales (Fig. 6). On the contrary, 87% and 73% of domestic dog detections were more frequent in cells with a decreasing proportion of natural vegetation and with an increasing percentage of pastures and crops at the buffer scale (Fig. 7). We did not find any relationship between the detections of Oncilla and the spatial variables evaluated.
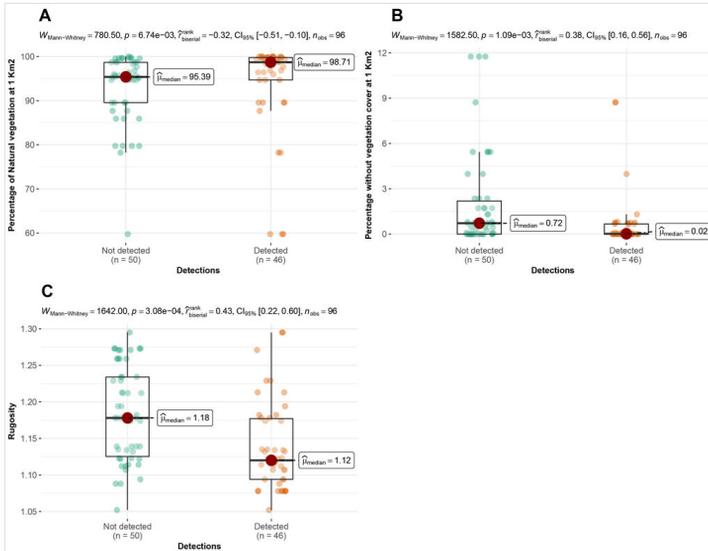
Figure 5. doi

Arrangement of detections of Andean bears according to the spatial variables in the Candelaria and Machay Reserves. **A** Detections according to the percentage of natural vegetation at 1 km^2; **B** Detections according to the percentage of the area without vegetation at 1 km^2; **C** Detections according to the rugosity index.
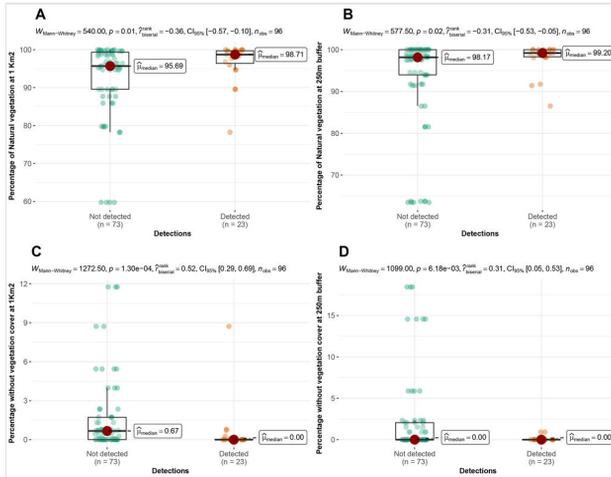
Figure 6. `doi`

Arrangement of detections of Pumas according to the spatial variables in the Candelaria and Machay Reserves. **A** Detections according to the percentage of natural vegetation at 1 km^2; **B** Detections according to the percentage of natural vegetation at 250 m buffer; **C** Detections according to the percentage of the area without vegetation at 1 km^2; **D** Detections according to the percentage of the area without vegetation at 250 m buffer.
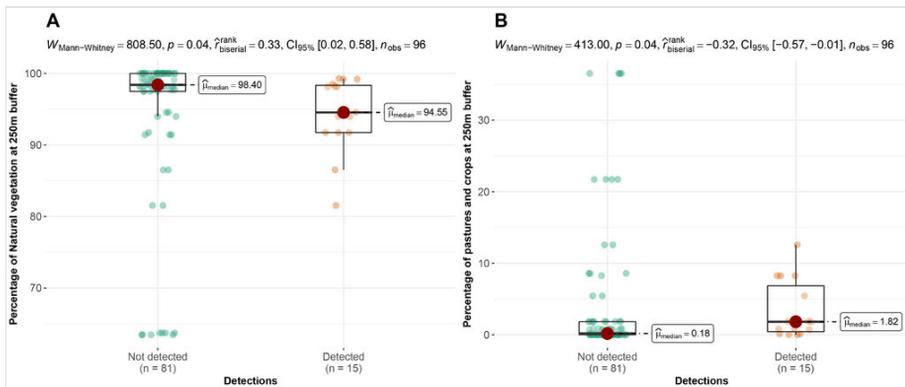
Figure 7. `doi`

Arrangement of detections of domestic dogs according to the spatial variables in the Candelaria and Machay Reserves. **A** Detections according to the percentage of natural vegetation at 250 m buffer; **B** Detections according to the percentage of pastures and crops at 250 m buffer.

Photo-identification

We reviewed 756 camera-trap records of Andean bears collected during the study, 72.5% of which correspond to the Candelaria Reserve and 27.5% to the Machay Reserve, comprising 135 independent records. We identified at least 26 Andean bears during the

study, 15 in the Candelaria and 11 in the Machay Reserve (Figs 8, 9). According to the sexual dimorphism, marking behaviour and body size, at least 53% of the individuals identified in the Candelaria and 45% in the Machay Reserve corresponded to adult males, while in the latter, only 27% of the individuals identified corresponded to subadults. Nevertheless, we were unable to identify females. In addition, we recorded seven recapture events of four individuals at the Candelaria (Fig. 10) and two recaptures of two individuals at the Machay Reserve between sampling campaigns (Fig. 11). We did not record recaptures of bears between Reserves during the study.

Figure 8. doi
Andean bears identified at the Candelaria Reserve, based on their natural facial marks. Letters correspond to different individuals identified during the study.

Figure 9. doi
Andean bears identified at the Machay Reserve, based on their natural facial marks. Letters correspond to different individuals identified during the study.

Figure 10. doi

Andean bears recaptured in different sampling campaigns at the Candelaria Reserve.

Figure 11. doi

Andean bears recaptured in different sampling campaigns at the Machay Reserve.
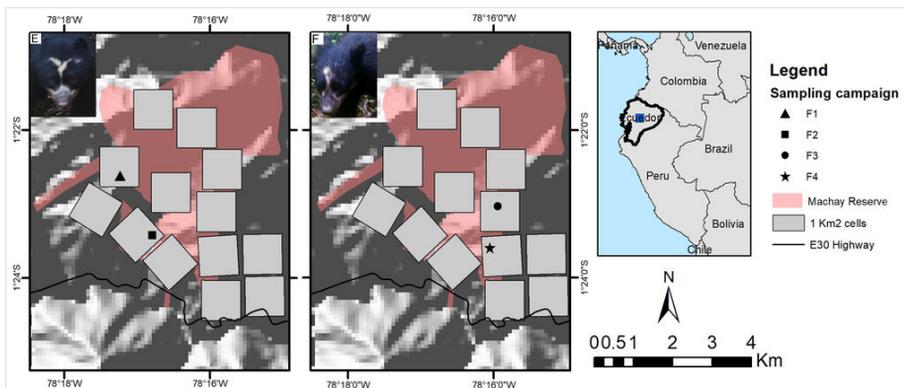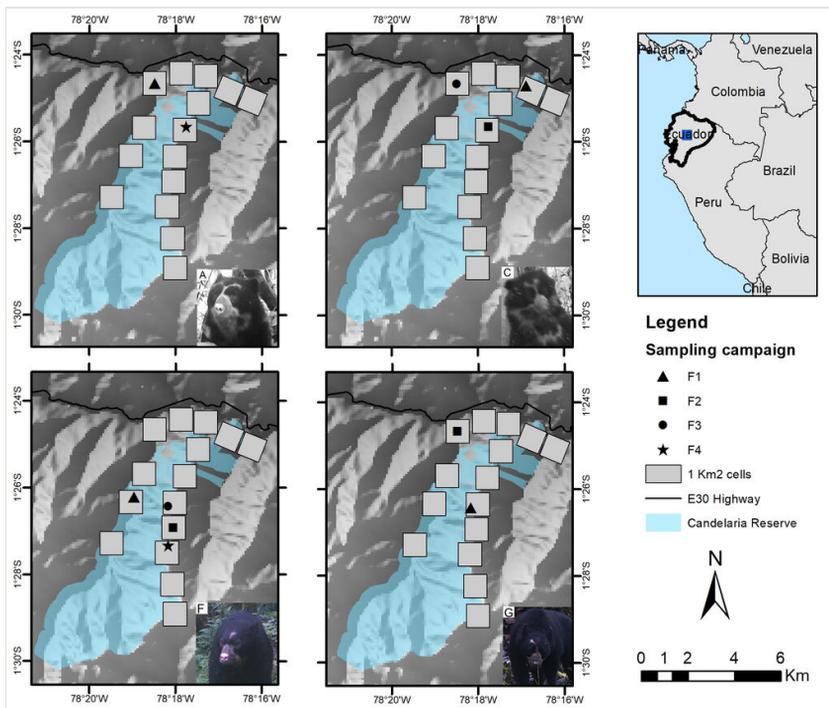
Discussion

The Andes of Ecuador, Peru and Bolivia are amongst the areas with the highest diversity and endemism of terrestrial mammals in the Neotropics (Ojeda 2013, Noguera-Urbano and

Escalante 2015). Our study constitutes the first long-term camera-trap monitoring study conducted in a strategic area that promotes the habitat connectivity between the Llanganates and Sangay National Parks in the eastern slopes of the Andes of Ecuador (i.e. CELS) (Lessmann et al. 2014, Cuesta et al. 2017). Our results reflected that the species richness of terrestrial mammals documented at the Candelaria and Machay Reserves is almost twice that of those recorded in a larger area in the Llanganates National Park (Palacios et al. 2018), although the sampling effort devoted in our study was greater (2320 trap-nights vs. 5232 trap-nights in our study) (Table 3). The diversity analysis showed that the species compositions recorded were moderately different in each Reserve, mainly due to species turnover, which may be a consequence of the species' ecological tolerance (Legendre 2014). For instance, we detected three unique species at the Candelaria Reserve, whereas five species were only detected at the Machay Reserve (Table 3). Our results revealed the dominance of Andean bears and domestic dogs in the study area (Fig. 3C). Accordingly, the relative abundance of Andean bears in our study greatly exceeded those reported by Palacios et al. (2018). We documented unprecedented detections of domestic dogs in the study area (Ríos Alvear and Reyes Puig 2013, Palacios et al. 2018), warning about the increasing human-associated disturbances and the negative interactions between wildlife and dogs (Lenth et al. 2008, Zapata-Ríos and Branch 2016). Similarly, this could have influenced the non-detection of other terrestrial mammals occurring in the study area (e.g. stripped hog-nosed skunk and Andean fox (Palacios et al. 2018)). In this regard, the lack of detections of mountain tapirs in camera traps during our study at the Candelaria Reserve is intriguing. This is not new, since previous camera-trap studies in Candelaria did not detect the species (Ríos Alvear and Reyes Puig 2013), even when there were identified eight different individuals at a 10 km distance in a smaller area and with less sampling effort than the current study (Reyes Puig and Ríos Alvear 2013). According to the species richness expected, we have recorded approximately 73% of the terrestrial mammal species in the area. We expect greater true species richness in the Machay Reserve since 42% of the species recorded are either rare (i.e. singletons and doubletons) or unique species (i.e. species recorded only in one Reserve) (Table 5).

The number of detections conditioned the species occupancy estimation since four of the 22 species documented contained 53% of the total detections during the study, while the 18 species remaining contributed between 0.2 and 6.6% of detections individually (Fig. 3 C). Additionally, due to the low sampling size, we were unable to identify covariate effects in the occupancy of the species modelled. However, the null model (i.e. which includes no covariates for detection and occupancy probabilities) revealed that the puma, oncilla and the Andean bear use between 30% and 60% of sampling units in the Candelaria and Machay Reserves, with the Andean bear the species with the highest detection probability (p = 0.27). The occupancy probability estimated for Andean bears in the Candelaria and Machay Reserves is similar to that observed by Springer (2018) in the Chocó-Andean region (Ψ = 0.6 our study vs. Ψ = 0.63) as well as the apparent positive effects of natural forests in the frequency of Andean bear detections within CELS. However, we surveyed a smaller area (78 km2 vs. 804.77 km2) and deployed half the number of camera traps (30 vs. 70 cameras). Our results suggest the occurrence of Andean bears in the Candelaria and Machay Reserves is not affected by the presence of humans and dogs (Springer 2018

, Rojas-VeraPinto et al. 2022), since we detected Andean bears close to human-associated features (e.g. roads, pastures and crops) and in camera-traps where we previously documented domestic dogs. However, this must be tested explicitly by, for example, assessing changes in the activity patterns which allows elucidating changes in the bear occurrence as a response to domestic dogs' presence (Zapata-Ríos and Branch 2016, Zapata-Ríos and Branch 2018). Moreover, the high frequency of detections in cells with a low proportion of vegetation absence may reflect the species' preference for areas that provide natural cover (García-Rangel 2012). However, inhabitants of El Placer, near the Candelaria Reserve, have observed Andean bears roaming through abandoned pastures and feeding on naranjilla crops (*Solanum quitoense*). In addition, we observed more detections in low rugosity areas, opposite to that reported by Rojas-VeraPinto et al. (2022), possibly due to the species exploiting crops for feeding resources (García-Rangel 2012). Detections of pumas were common in cells with almost complete natural vegetation cover and without open areas, suggesting the species evade human disturbance, opposite to what was observed by Figel et al. (2021). On the contrary, our observations suggest that domestic dogs roam in natural habitats close to areas associated with human presence (e.g. pastures and crops) (Paschoal et al. 2018, Zapata-Ríos and Branch 2018). Thus, even though we did not identify explicit effects of the presence of domestic dogs on the probability of pumas occupancy, the spatial arrangement of puma detections does not coincide with the areas where domestic dogs were more frequently detected, suggesting puma's avoidance behaviour of dogs (Zapata-Ríos and Branch 2018).

The number of Andean bears identified in our study exceeds that documented by Molina et al. (2017) in the Chocó-Andean region and doubles that observed in a previous study at the Candelaria Reserve (Ríos Alvear and Reyes Puig 2013), although our sampling effort was greater (1224, 1050 and 5232 trap-nights, respectively). We are convinced that the true number of bears in the study area is larger than the observed number since we excluded the poor-resolution camera trap records of Andean bears to prevent uncertainty in the photo identification. We recaptured six Andean bears during our study, both in consecutive sampling campaigns and throughout the entire fieldwork (Figs 10, 11). In addition, we suspect the individual C, recorded at the Candelaria Reserve, was previously detected in a survey at the Chamanapamba Natural Reserve in 2011, 10 km to the west of our study area (Ríos Alvear and Reyes Puig 2013) (Fig. 12). To our knowledge, this record depicts the oldest recapture of an Andean bear after eleven years. Due to the individuals identified, our study suggests that Candelaria, Machay and Chamanapamba Reserves, as well as many other natural vegetation remnants within CELS, support the occurrence of landscape species (e.g. Andean bear) and would potentially contribute to the wildlife dispersal between protected areas (Sanderson et al. 2002, Crespo-Gascón and Guerrero-Casado 2019). Additionally, these areas are important refuges of suitable habitats that provide resting and foraging areas for terrestrial mammals within CELS and are critical for managing the habitat connectivity between the Llanganates and Sangay National Parks (Reyes Puig and Ríos Alvear 2013, Ríos Alvear and Reyes Puig 2013, Lessmann et al. 2014, Reyes-Puig et al. 2015, Ríos-Alvear and Reyes-Puig 2015, Cuesta et al. 2017).

Our study highlights the importance of the Candelaria and Machay Reserves as highly diverse areas encroaching in a human-dominated landscape. We expect our results serve as a starting point for establishing a participative landscape scale monitoring network promoting the involvement of conservationists and private stakeholders in CELS. We expect our results to contribute to strengthening the management capacity in the Llanganates and Sangay National Parks, allowing park managers to capitalise on conservation outcomes through coordinated work with local conservationists. In addition, we expect local governments to take advantage of our information to make informed decisions regarding the land-use change and management taking into account the importance of private reserves for strenghthening the habitat connectivity and supporting the endeavour of local conservationists within CELS.

Figure 12. doi

Recapture of an Andean bear recorded in 2011 at the Chamanapamba Natural Reserve (Ríos Alvear and Reyes Puig 2013) (**left**) and the individual C recorded at the Candelaria Reserve in our study (**right**).

Acknowledgements

References

- Albert CH, Rayfield B, Dumitru M, Gonzalez A (2017) Applying network theory to prioritize multispecies habitat networks that are robust to climate and land-use change. Conservation Biology 31 (6): 1383-1396. https://doi.org/10.1111/cobi.12943
- Beier P, Noss R (1998) Do habitat corridors provide connectivity? Conservation Biology 12 (6): 1241-1252. https://doi.org/https://doi.org/10.1111/j.1523-1739.1998.98036.x
- Beier P, Spencer W, Baldwin RF, McRae BH (2011) Toward best practices for developing regional connectivity maps. Conservation Biology 25 (5): 879-92. https://doi.org/10.1111/j.1523-1739.2011.01716.x
- Belote RT, Dietz MS, McRae BH, Theobald DM, McClure ML, Irwin GH, McKinley PS, Gage JA, Aplet GH (2016) Identifying corridors among large protected areas in the United States. PLOS One 11 (4). https://doi.org/10.1371/journal.pone.0154223
- Beyer HL, Gurarie E, Borger L, Panzacchi M, Basille M, Herfindal I, Van Moorter B, S RL, Matthiopoulos J (2016) 'You shall not pass!': quantifying barrier permeability and proximity avoidance by animals. Journal of Animal Ecology 85 (1): 43-53. https://doi.org/10.1111/1365-2656.12275
- Cardoso P, Rigal F, Carvalho J, Fortelius M, Borges PV, Podani J, Schmera D (2014) Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. Journal of Biogeography 41 (4): 749-761. https://doi.org/10.1111/jbi.12239
- Cardoso P, Rigal F, Carvalho J (2015) BAT – Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. Methods in Ecology and Evolution 6 (2): 232-236. https://doi.org/10.1111/2041-210X.12310
- Carvalho J, Cardoso P, Gomes P (2012) Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. Global Ecology and Biogeography 21 (7): 760-771. https://doi.org/10.1111/j.1466-8238.2011.00694.x
- Cavelier J, Lizcano D, Yerena E, Downer C (2011) The mountain tapir (*Tapirus pinchaque*) and Andean bear (*Tremarctos ornatus*): two charismatic, large mammals in South American tropical montane cloud forests. In: Scatena FN, Bruijnzeel LA, Hamilton LS (Eds) Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge University Press, Cambridge, 9 pp. [ISBN 9780521760355]. https://doi.org/10.1017/CBO9780511778384.019
- Chao A, Chiu C, Jost L (2014a) Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. Annual Review of Ecology, Evolution, and Systematics 45 (1): 297-324. https://doi.org/10.1146/annurev-ecolsys-120213-091540
- Chao A, Gotelli N, Hsieh TC, Sander E, Ma KH, Colwell R, Ellison A (2014b) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84 (1): 45-67. https://doi.org/10.1890/13-0133.1

- Crespo-Gascón S, Guerrero-Casado J (2019) The role of the spectacled bear (*Tremarctos ornatus*) as an umbrella species for Andean ecoregions. Wildlife Research 46 (2): 176-183. https://doi.org/10.1071/WR18056
- Crespo PJ, Feyen J, Buytaert W, Bücker A, Breuer L, Frede H, Ramírez M (2011) Identifying controls of the rainfall–runoff response of small catchments in the tropical Andes (Ecuador). Journal of Hydrology 407 (1): 164-174. https://doi.org/10.1016/j.jhydrol.2011.07.021
- Cuesta F, Peralvo M, Merino-Viteri A, Bustamante M, Baquero F, Freile J, Muriel P, Torres-Carvajal O (2017) Priority areas for biodiversity conservation in mainland Ecuador. Neotropical Biodiversity 3 (1): 93-106. https://doi.org/10.1080/23766808.2017.1295705
- Dinno A, Dinno MA (2017) Package 'dunn. test'. CRAN Repos 10: 1-7. URL: https://cran.r-project.org/package=dunn.test
- Figel J, Botero S, Sánchez-Londoño J, Racero-Casarrubia J (2021) Jaguars and pumas exhibit distinct spatiotemporal responses to human disturbances in Colombia's most imperiled ecoregion. Journal of Mammalogy 102 https://doi.org/10.1093/jmammal/gyaa146
- Fletcher RJJ, Sefair JA, Wang C, Poli CL, Smith TAH, Bruna EM, Holt RD, Barfield M, Marx AJ, Acevedo MA (2019) Towards a unified framework for connectivity that disentangles movement and mortality in space and time. Ecology Letters 22 (10): 1680-1689. https://doi.org/10.1111/ele.13333
- Gaglio M, Aschonitis VG, Mancuso MM, Reyes Puig JP, Moscoso F, Castaldelli G, Fano EA (2017) Changes in land use and ecosystem services in tropical forest areas: a case study in Andes mountains of Ecuador. International Journal of Biodiversity Science, Ecosystem Services & Management 13 (1): 264-279. https://doi.org/10.1080/21513732.2017.1345980
- García-Rangel S (2012) Andean bear *Tremarctos ornatus* natural history and conservation. Mammal Review 42 (2): 85-119. https://doi.org/10.1111/j.1365-2907.2011.00207.x
- Goodwin B, Fahrig L (2002) How does landscape structure influence landscape connectivity? Oikos 99 (3): 552-570. https://doi.org/10.1034/j.1600-0706.2002.11824.x
- Gotelli N, Chao A (2013) Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. In: Levin S (Ed.) Encyclopedia of Biodiversity (Second Edition). Academic Press, Waltham, 16 pp. [ISBN 978-0-12-384720-1]. https://doi.org/10.1016/B978-0-12-384719-5.00424-X
- Gradstein SR, Reiner-Drehwald ME, Jost L (2004) The systematic position and distribution of *Myriocolea irrorata* (Lejeuneaceae), an endangered liverwort of the Ecuadorian Andes. The Journal of the Hattori Botanical Laboratory 95: 235-248. https://doi.org/10.18968/jhbl.95.0_235
- Grantham HS, Duncan A, Evans TD, Jones KR, Beyer HL, Schuster R, Walston J, Ray JC, Robinson JG, Callow M, Clements T, Costa HM, DeGemmis A, Elsen PR, Ervin J, Franco P, Goldman E, Goetz S, Hansen A, Hofsvang E, Jantz P, Jupiter S, Kang A, Langhammer P, Laurance WF, Lieberman S, Linkie M, Malhi Y, Maxwell S, Mendez M, Mittermeier R, Murray NJ, Possingham H, Radachowsky J, Saatchi S, Samper C, Silverman J, Shapiro A, Strassburg B, Stevens T, Stokes E, Taylor R, Tear T, Tizard R, Venter O, Visconti P, Wang S, Watson JEM (2020) Anthropogenic modification of forests

means only 40% of remaining forests have high ecosystem integrity. Nature Communications 11 (1). https://doi.org/10.1038/s41467-020-19493-3

- Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG (2013) High-resolution global maps of 21st-century forest cover change. Science 342 (6160): 850-853. https://doi.org/10.1126/science.1244693
- Herrera L, Sabatino M, Jaimes F, Saura S (2017) Landscape connectivity and the role of small habitat patches as stepping stones: an assessment of the grassland biome in South America. Biodiversity and Conservation 26 (14): 3465-3479. https://doi.org/10.1007/s10531-017-1416-7
- Horn RV, Zug B, LaCombe C, Velez-Liendo X, Paisley S (2014) Human visual identification of individual Andean bears *Tremarctos ornatus*. Wildlife Biology 20 (5): 291-299. https://doi.org/10.2981/wlb.00023
- Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7 (12): 1451-1456. https://doi.org/10.1111/2041-210X.12613
- Ilbay-Yupa M, Lavado-Casimiro W, Rau P, Zubieta R, Castillón F (2021) Updating regionalization of precipitation in Ecuador. Theoretical and Applied Climatology 143 (3): 1513-1528. https://doi.org/10.1007/s00704-020-03476-x
- INAMHI, National Institute of Meteorology and Hydrology- Ecuador (2022) Red de estaciones automáticas hidrometeorológicas. URL: http://186.42.174.236/InamhiEmas/#
- Jost L (2004) Explosive local radiation of the genus *Teagueia* (Orchidaceae) in the Upper Pastaza watershed of Ecuador. Lyonia 7 (1): 41-47. URL: https://www.lyonia.org/articles/rbussmann/article_323/pdf/article.pdf
- Jost L (2006) Entropy and diversity. Oikos 113 (2): 363-375. https://doi.org/10.1111/j.2006.0030-1299.14714.x
- Jost L, Shepard A (2017) Four new *Teagueia* (Orchidaceae: Pleurothallidinae) from the upper Río Pastaza watershed of East-Central Ecuador. Lankesteriana 17: 261-278. URL: http://www.scielo.sa.cr/scielo.php?script=sci_arttext&pid=S1409-38712017000200261&nrm=iso
- Krausman PR (1999) Some basic principles of habitat use. In: Launchbaugh KL, Sanders KD, Mosley JL (Eds) Grazing Behaviour of Livestock and Wildlife. 70. University of Idaho, Moscow, ID, 5 pp. URL: https://www.lib.uidaho.edu/digital/fwres/items/fwres42.html
- Laurance WF, Goosem M, Laurance SG (2009) Impacts of roads and linear clearings on tropical forests. Trends in Ecology and Evolution 24 (12): 659-69. https://doi.org/10.1016/j.tree.2009.06.009
- Lawler JJ, Ruesch AS, Olden JD, McRae BH (2013) Projected climate-driven faunal movement routes. Ecology Letters 16 (8): 1014-22. https://doi.org/10.1111/ele.12132
- Legendre P (2014) Interpreting the replacement and richness difference components of beta diversity. Global Ecology and Biogeography 23 (11): 1324-1334. https://doi.org/10.1111/geb.12207
- Lenth B, Knight R, Brennan M (2008) The effects of dogs on wildlife communities. Natural Areas Journal 28 (3): 218-227. https://doi.org/10.3375/0885-8608(2008)28[218:Teodow]2.0.Co;2

- Leonard PB, Sutherland RW, Baldwin RF, Fedak DA, Carnes RG, Montgomery AP (2017) Landscape connectivity losses due to sea level rise and land use change. Animal Conservation 20 (1): 80-90. https://doi.org/10.1111/acv.12289
- Lessmann J, Muñoz J, Bonaccorso E (2014) Maximizing species conservation in continental Ecuador: a case of systematic conservation planning for biodiverse regions. Ecology and Evolution 4 (12): 2410-2422. https://doi.org/10.1002/ece3.1102
- Lopez de Vargas Machuca K (2014) Diseño de corredores biológicos para mamíferos entre los Parques Nacionales Llanganates y Sangay, Ecuador. Universidad Internacional Menéndez Pelayo, Quito, Ecuador. URL: https://www.researchgate.net/publication/322632636_DISENO_DE_CORREDORES_BIOLOGICOS_PARA_MAMIFEROS_ENTRE_LOS_PARC
- MacKenzie D, Nichols J, Lachman G, Droege S, Andrew Royle J, Langtimm C (2002) Estimating site occupancy rates when detection probabilities are less than one. Ecology 83 (8): 2248-2255. https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2
- MacKenzie D, Bailey L (2004) Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics 9 (3): 300-318. https://doi.org/10.1198/108571104x3361
- MacKenzie D, Nichols J, Royle JA, Pollock K, Bailey L, Hines J (2018) Chapter 2 - Occupancy applications. In: MacKenzie D, Nichols J, Royle JA, Pollock K, Bailey L, Hines J (Eds) Occupancy Estimation and Modeling (Second Edition). Academic Press, Boston, 43 pp. [ISBN 978-0-12-407197-1]. https://doi.org/10.1016/B978-0-12-407197-1.00003-X
- Marrotte RR, Bowman J, Brown MGC, Cordes C, Morris KY, Prentice MB, Wilson PJ (2017) Multi-species genetic connectivity in a terrestrial habitat network. Movement Ecology 5 https://doi.org/10.1186/s40462-017-0112-2
- Medrano-Vizcaíno P, Espinosa S (2021) Geography of roadkills within the Tropical Andes Biodiversity Hotspot: poorly known vertebrates are part of the toll. Biotropica 53 (3): 820-830. https://doi.org/10.1111/btp.12938
- Metzger J, Décamps H (1997) The structural connectivity threshold: An hypothesis in conservation biology at the landscape scale. Acta Oecologica 18 (1): 1-12. https://doi.org/10.1016/S1146-609X(97)80075-6
- Molina S, Fuller A, Morin D, Royle JA (2017) Use of spatial capture–recapture to estimate density of Andean bears in northern Ecuador. Ursus 28 (1): 117-126. https://doi.org/10.2192/URSU-D-16-00030.1
- Myers N, Mittermeier R, Mittermeier C, da Fonseca GB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403 (6772): 853-858. https://doi.org/10.1038/35002501
- Newbold T, Hudson LN, Hill SL, Contu S, Lysenko I, Senior RA, Borger L, Bennett DJ, Choimes A, Collen B, Day J, De Palma A, Diaz S, Echeverria-Londono S, Edgar MJ, Feldman A, Garon M, Harrison ML, Alhusseini T, Ingram DJ, Itescu Y, Kattge J, Kemp V, Kirkpatrick L, Kleyer M, Correia DL, Martin CD, Meiri S, Novosolov M, Pan Y, Phillips HR, Purves DW, Robinson A, Simpson J, Tuck SL, Weiher E, White HJ, Ewers RM, Mace GM, Scharlemann JP, Purvis A (2015) Global effects of land use on local terrestrial biodiversity. Nature 520 (7545): 45-50. https://doi.org/10.1038/nature14324
- Nielsen S, McDermid G, Stenhouse G, Boyce M (2010) Dynamic wildlife habitat models: Seasonal foods and mortality risk predict occupancy-abundance and habitat

- selection in grizzly bears. Biological Conservation 143 (7): 1623-1634. https://doi.org/10.1016/j.biocon.2010.04.007
- Noguera-Urbano EA, Escalante T (2015) Áreas de endemismo de los mamíferos (Mammalia) Neotropicales. Acta Biológica Colombiana 20: 47-65. https://doi.org/10.15446/abc.v20n3.46179
- Ojeda R (2013) Diversity and Conservation of Neotropical Mammals. In: Levin S (Ed.) Encyclopedia of biodiversity (Second Edition). Academic Press, Waltham, 12 pp. [ISBN 978-0-12-384720-1]. https://doi.org/10.1016/B978-0-12-384719-5.00353-1
- Oksanen J, Kindt R, Legendre P, Hara B, Henry M, Stevens H (2007) The vegan package. CRAN Repositor URL: https://cran.r-project.org/web/packages/vegan/vegan.pdf
- Palacios J, Naveda-Rodríguez A, Zapata-Ríos G (2018) Large mammal richness in Llanganates National Park, Ecuador. Mammalia 82 (4): 309-314. https://doi.org/10.1515/mammalia-2017-0071
- Paschoal AO, Massara R, Bailey L, Doherty P, Santos P, Paglia A, Hirsch A, Chiarello A (2018) Anthropogenic disturbances drive domestic dog use of Atlantic Forest protected areas. Tropical Conservation Science 11 https://doi.org/10.1177/1940082918789833
- Patil I (2021) Visualizations with statistical details: The 'ggstatsplot' approach. Journal of Open Source Software 6 (61). https://doi.org/10.21105/joss.03167
- Pereira H, Navarro L, Martins I (2012) Global Biodiversity Change: The bad, the good, and the unknown. The Annual Review of Environment and Resources 37: 25-50. https://doi.org/10.1146/annurev-environ-042911-093511
- RAISG (2020) Deforestación en la Amazonía 2000 - 2018. Red Amazónica de Información Socioambiental Georreferenciada. URL: https://www.amazoniasocioambiental.org/es/publicacion/nota-tecnica-deforestacion-en-la-amazonia-2000-2018/
- Reyes Puig C, Ríos Alvear G (2013) Monitoreo del tapir de montaña (*Tapirus pinchaque*) en el bosque nublado de la Reserva Natural Chamanapamba. Boletín Técnico, Serie Zoológica 11 (8-9): 74-90. URL: https://journal.espe.edu.ec/ojs/index.php/revista-serie-zoologica/article/view/1457/1041
- Reyes-Puig CP, Ríos-Alvear GD, Reyes-Puig JP (2015) Notable ampliación del rango altitudinal de *Eira barbara* Cabeza de Mate (Mammalia: Mustelidae). ACI Avances en Ciencias e Ingenierías 7 (1). https://doi.org/10.18272/aci.v7i1.229
- Reyes-Puig JP, Reyes-Puig C, Franco-Mena D, Jost L, Yánez-Muñoz M (2022) Strong differentiation between amphibian communities on two adjacent mountains in the Upper Rio Pastaza watershed of Ecuador, with descriptions of two new species of terrestrial frogs. ZooKeys 1081: 35-87. https://doi.org/10.3897/zookeys.1081.71488
- Ríos Alvear G, Reyes Puig C (2013) Monitoreo del oso andino (*Tremarctos ornatus*) en tres áreas de bosque nublado en la cuenca alta del Pastaza. Boletín Técnico, Serie Zoológica 11 (8-9): 91-108. URL: https://journal.espe.edu.ec/ojs/index.php/revista-serie-zoologica/article/view/1458/1043
- Ríos-Alvear G, Reyes-Puig C (2015) Corredor ecológico Llanganates-Sangay: Un acercamiento hacia su manejo y funcionalidad. Yachana Revista Científica 4 (2). https://doi.org/10.1234/ych.v4i2.220
- Ríos-Franco C, Franco P, Forero-Medina G (2013) Toolbox for the identification of priority areas for conservation. GIS dynamical Model V1. 0. Wildlife Conservation

Society Colombia URL: https://programs.wcs.org/beta/Resources/Publications/Publications-Search-II/ctl/view/mid/13340/pubid/DMX1529300000.aspx

- Rodriguez D, Reyes A, Tarquino-Carbonell AdP, Restrepo H, Reyes-Amaya N (2021) Space use by a male Andean bear (*Tremarctos ornatus*) tracked with GPS telemetry in the Macizo Chingaza, Cordillera Oriental of the Colombian Andes. Notas sobre Mamíferos Sudamericanos 3 https://doi.org/10.31687/saremNMS.21.2.4

- Rojas-VeraPinto R, Bautista C, Selva N (2022) Living high and at risk: predicting Andean bear occurrence and conflicts with humans in southeastern Peru. Global Ecology and Conservation 36 https://doi.org/10.1016/j.gecco.2022.e02112

- Rovero F, Marshall A (2009) Camera trapping photographic rate as an index of density in forest ungulates. Journal of Applied Ecology 46 (5): 1011-1017. https://doi.org/10.1111/j.1365-2664.2009.01705.x

- Sánchez D, Merlo J, Haro R, Acosta M, Bernal G (2018) Soils from the Amazonia. In: Espinosa J, Moreno J, Bernal G (Eds) The Soils of Ecuador. Springer International Publishing, Cham, 24 pp. [ISBN 978-3-319-25319-0]. https://doi.org/10.1007/978-3-319-25319-0_4

- Sanderson E, Redford K, Vedder A, Coppolillo P, Ward S (2002) A conceptual model for conservation planning based on landscape species requirements. Landscape and Urban Planning 58 (1): 41-56. https://doi.org/10.1016/S0169-2046(01)00231-6

- Seidler RG, Long RA, Berger J, Bergen S, Beckmann JP (2015) Identifying impediments to long-distance mammal migrations. Conservation Biology 29 (1): 99-109. https://doi.org/10.1111/cobi.12376

- Simpson B (1975) Pleistocene changes in the flora of the high Tropical Andes. Paleobiology 1 (3): 273-294. https://doi.org/10.1017/S0094837300002530

- Smith B, Wilson JB (1996) A consumer's guide to evenness indices. Oikos 76: 70-82. https://doi.org/10.2307/3545749

- Springer V (2018) Occupancy and co-occurence of carnivores in the Ecuadorian Andes. Cornell University, New York, USA. https://doi.org/10.7298/nmws-7m86

- Zapata-Ríos G, Branch L (2016) Altered activity patterns and reduced abundance of native mammals in sites with feral dogs in the high Andes. Biological Conservation 193: 9-16. https://doi.org/10.1016/j.biocon.2015.10.016

- Zapata-Ríos G, Branch L (2018) Mammalian carnivore occupancy is inversely related to presence of domestic dogs in the high Andes of Ecuador. PLOS ONE 13 (2). https://doi.org/10.1371/journal.pone.0192346

- Zeller K, McGarigal K, Whiteley A (2012) Estimating landscape resistance to movement: a review. Landscape Ecology 27 (6): 777-797. https://doi.org/10.1007/s10980-012-9737-0

Supplementary materials

Suppl. material 1: SM1 `doi`

Authors: Carolina Reyes-Puig, Gorky Ríos Alvear, and Juan Pablo Reyes Puig
Data type: Beta diversity coefficients
Brief description: Accumulated beta diversity considering the beta diversity partitioning approach.
Download file (13.81 kb)

Suppl. material 2: Detailed outcomes of the occupancy models assessed. `doi`

Authors: Gorky Ríos-Alvear
Data type: Occupancy modelling outcomes
Download file (186.24 kb)