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Research Article

Distribution, abundance, and spatial ecology of the critically endangered Ecuadorian capuchin (*Cebus albifrons aequatorialis*)

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Abstract

Geographically isolated from other *C. albifrons* taxa found east of the Andes, the Ecuadorian capuchin (*Cebus albifrons aequatorialis*) is a Critically Endangered primate that survives in a small number of localities in western Ecuador and extreme northern Peru. We assessed 11 forested areas in western Ecuador to determine presence/absence using a combination of on-foot searching and interviews with local informants. *C. a. aequatorialis* were present at seven of the sites surveyed, four of which represent new presence localities. We carried out extensive censuses of five small, private reserves to obtain estimates of population density and demographic information. We also examined home range characteristics and habitat selection at one well-studied site. Population densities based on absolute counts at these sites ranged from 2 - 22 individuals/km² (median = 2.4). Jauneche, a 138 ha isolated fragment reserve with 22 individuals/km², was a clear outlier. Although we observed some solitary individuals, *C. a. aequatorialis* live predominantly in multi-male multi-female social groups, with a mean group size of 13.9 (range 5-20). The composition of social groups was typical for *Cebus*: adult females outnumbered adult males slightly, and groups exhibited relatively high immature to adult female ratios (mean = 1.5). Home ranges were unusually large for the genus (507 – 561 ha). The capuchins exhibited strongest selection for mature forest near streams, although they also used degraded forest frequently. *C. a. aequatorialis* faces critical threats in the form of habitat loss, hunting, and harassment by farmers, but we suggest that some remaining populations have the potential to grow if effective protection can be established.

Key Words: habitat fragmentation, census, habitat loss, conservation, demography

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Introduction

Untufted capuchins (*Cebus spp.*) are widely distributed throughout Central and South America, and they have traditionally been separated by taxonomists into three groups: the white-fronted capuchin (*C. albifrons*), the wedge-capped capuchin (*C. olivaceus*), and the white-faced capuchin (*C. capucinus*) [1]. Although the systematics of the untufted capuchins remains unclear, there is growing evidence that some or all of these traditionally recognized species are paraphyletic and that a major reorganization of *Cebus* taxonomy may be needed [see recent reviews by 2,3,4]. The Ecuadorian capuchin [*Cebus albifrons aequatorialis*: 5], which is indigenous to western Ecuador and northernmost Peru, is among the most universally recognized and undisputed taxa of those formerly ascribed to *C. albifrons* [1,6,7]. Using genetic data, two recent attempts [3,4] to resolve the phylogenetic relationships among the untufted capuchins were inconclusive with regard to *C. a. aequatorialis*. The analysis by Ruiz-García et al. [3] suggested that *C. a. aequatorialis* is most closely related to specimens from widely separated localities including the central Peruvian Amazon, southern and eastern Colombia, westernmost Brazil, and French Guyana. These apparent genetic affinities varied extensively with the analysis methods used and are difficult to reconcile with the geographic separation of these samples. The specimen of *C. a. aequatorialis* used by Boubli et al. [4] was a zoo animal, and the authors believe that it was mislabeled representative of *C. capucinus*. The taxonomic status of *C. a. aequatorialis* is therefore best considered unresolved [3,4]. Given its geographical separation from other recognized *C. albifrons* populations by the Andes mountain range and the suggestion by Boubli et al. [4] to elevate many of these putative subspecies to the species level based on the phylogenetic species concept, it is likely that *C. a. aequatorialis* deserves its own species distinction.

Distribution maps depict *C. a. aequatorialis* as occurring throughout western Ecuador, from sea level to less than 2000 meters on the western slopes of the Andean Cordillera Occidental [1,8,9], but the limits of its range to the north and south are uncertain [7]. Some taxonomists have speculated that its northern range may overlap with that of *C. capucinus* in northwestern Ecuador and that the two species may hybridize [10]. Older distribution maps [e.g. 1,8] consider the southern range to end just south of Guayaquil in the province of Guayas, but Albuja and Arcos [11], Cornejo and de la Torre [12], and Encarnación and Cook [13] report that *C. a. aequatorialis* inhabits more southerly forested areas in Ecuador and in the Tumbes department of northern Peru.

The most comprehensive published survey of *C. a. aequatorialis* in Ecuador lists 13 inhabited localities [11] that range from nationally protected parks and small private reserves to unprotected forest fragments. In 2008, the IUCN conservation status of *C. a. aequatorialis* was revised from Near Threatened to Critically Endangered [12,14], due in large part to the catastrophic habitat loss that has occurred in the western lowlands of Ecuador over the last half-century [15,16]. Cornejo and de la Torre [12] state that populations of *C. a. aequatorialis* remain in fewer than 10 protected areas across its entire geographic range, and the remaining populations face a variety of threats including habitat loss, hunting, and illegal trade [16]. The IUCN assessment is based on scant evidence, as published estimates of population sizes and densities, which are all based on a very small number of actual sightings, are available for only four localities [Cordillera de Jama and El Palmar: 11,Jauneche: 17,El Pital: 18]. With regard to primates in western Ecuador, de la Torre [16, p. 4] states that “there is almost no information about the population status of the species in any of the areas” with which to evaluate potential conservation plans.

Here, we present new data on the distribution and abundance of *C. a. aequatorialis* in western Ecuador. We describe several localities for which the presence of *C. a. aequatorialis* has not been previously documented, and we describe the range of habitats occupied and the total geographic extent of the subspecies. We give population density estimates and describe basic demographic patterns at several intensively surveyed sites,

and home range characteristics and habitat preferences for two groups at one well-studied location. Although these data are now several years old, they remain relevant as there are no comparable data available for *C. a. aequatorialis*. To our knowledge, there have been no targeted efforts at conserving *C. a. aequatorialis*, and our primary aim is to provide the basic socioecological information required to guide conservation decisions and enact effective conservation plans for this little-known primate.

Methods

Presence/absence localities

We assessed 11 sites in western Ecuador (Fig. 1, Table 1) for the presence of *C. a. aequatorialis* between 2002 and 2005 using a combination of on-site searching and interviews with local informants. We selected several of these sites with the ultimate goal of habituating one or more groups for a behavioral and ecological study. Hence, some of the sites were selected because they appeared suitable—based on local infrastructure, vegetation maps of the region, informants, and previously published reports—for accommodating a research program. The range of habitats encompassed by these sites includes Ecuadorian dry forest, mangrove forest, mature moist forest, undisturbed Chocó rainforest, and premontane forest. We classified sites as presence localities if we could visually confirm the presence of *C. a. aequatorialis* or if local informants reported seeing them in the recent past (<1 year). We classified sites as absence localities if we were unable to find *C. a. aequatorialis* during our searching and if no local informant had seen them in at least 5 years. During our interviews with local informants we first asked if there were monkeys present in the area. If they said yes, we then asked them to describe 1) the physical characteristics of the different monkeys they had seen, 2) where they had seen the monkeys, and 3) how much time had passed since their most recent sighting. Since Cotacachi-Cayapas was suspected to have both *C. a. aequatorialis* and *C. capucinus*, we also asked informants in this area who had seen capuchin monkeys to indicate which species using color illustrations in a field guide [19].

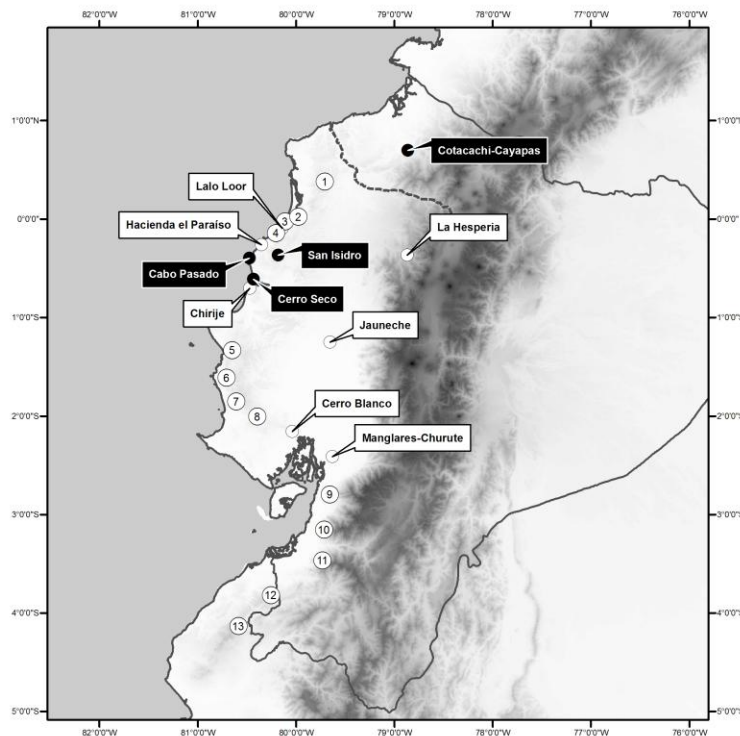


Fig. 1 Survey localities and all known presence localities in the geographic range of *Cebus albifrons aequatorialis*. Localities labeled with names were surveyed in this study. White labels indicate presence and black labels indicate absence of *C. a. aequatorialis*. The dotted line represents the Esmeraldas-Guayllabamba River, which likely forms the northern limit of the subspecies' range. Localities labeled with numbers have been previously published [11 - 13, 17, 18, 31]: 1 Bilsa Biological Reserve, 2 Pata de Pájaro, 3 El Palmar, 4 Tito Santos Biological Reserve, 5 La Planada, 6 Machalilla National Park, 7 Loma Alta Ecological Reserve, 8 Cordillera La Tapada, 9 Cooperativa Nueva Naranjal, 10 Cooperativa 31 de Agosto, 11 Cerro Azul, 12 Tumbes Reserved Zone, 13 Cerros de Amotape National Park.

Surveys and intensive population censuses

We carried out searching on foot at all sites except for Cotacachi-Cayapas and Manglares-Churute. The timeframe of our study did not allow us to attempt thorough censuses of these two nationally-protected sites, as both are large (3,044 km² and 350 km², respectively) and relatively inaccessible. Therefore, we relied primarily on local informants simply to establish presence or absence at these two sites. At the other nine sites, search effort varied roughly in proportion to the size of the forested area (Table 2). Our preliminary survey attempts suggested that distance sampling along line transects [20] might be inadequate for our study. First, the monkeys almost always detected us and began to flee before we detected them. This violated three key assumptions of distance sampling: that groups are detected at their initial locations before responding to the observer, that distance to the group center is recorded accurately, and that group size is recorded accurately [20]. If we had restricted our searches to line transects, we would not have been able to record group sizes and compositions accurately. Second, encounter rates were extremely low (e.g. one encounter for every 56 hours of searching at Hacienda Paraíso), and the terrain at most sites was rugged. Peck et al. [21] note that using line transect sampling to obtain confident estimates of population density for rare and widely-dispersed animals in steep terrain can require a very large sampling effort. Third, the areas surveyed were relatively small forest fragments (138 – 2929 ha), and each site contained only a small number of *C. a. aequatorialis* groups. Re-sighted groups were usually recognizable by their distinctive adult males (see below), and the populations at the survey sites were effectively closed during the sampling period because of deforestation outside of fragments. These conditions suggested that an effective alternative to transect-based sampling would be complete-count censuses [22], in which all distinct groups in a discrete forested area were identified and their individuals counted.

Table 1. Survey localities for *Cebus albifrons aequatorialis* (C. a. a).

Site	Latitude	Longitude	Present/ absent	Means of validation
Cabo Pasado	-0.39605	-80.47390	Absent	Visual and informant
Cerro Blanco Protected Forest	-2.15775	-80.04076	Present	Visual and published [17]
Cerro Seco Biological Reserve	-0.61103	-80.43605	Absent	Visual and informant
Chirije	-0.70270	-80.47306	Present	Visual and informant
Cotacachi-Cayapas National Park	0.69761	-78.86363	Absent	Informant and published [12]
Hacienda Paraíso	-0.26006	-80.35264	Present	Visual
Jauneche	-1.24866	-79.65691	Present	Visual and published [17]
La Hesperia Biological Reserve	-0.36652	-78.86958	Present	Visual
Lalo Loor Dry Forest Reserve	-0.09510	-80.14211	Present	Visual
Manglares-Churute National Park	-2.41250	-79.63384	Present	Informant and published [12]
San Isidro	-0.36667	-80.18334	Absent	Visual and informant

Searching teams of 2-4 observers walked roads, trails, cattle paths, fence lines, and stream beds in one area of the reserve throughout the day. We relied on local guides and on topographic vegetation maps to plan search routes. On a typical day, we searched for 4-5 hours in the morning in one area and 2-3 hours in the late afternoon in a different area. When a group was found, its location was recorded with a Garmin GPS 12, and group members were counted and age/sex compositions recorded. When possible, these counts were confirmed by two observers and repeated until stable counts were obtained. Age/sex compositions included the following categories: adult male (≥ 10 years), adult female (≥ 6 years), subadult male (6-9 years), juvenile

(1-5 years), and infant (<1 year). Capuchins of these age/sex categories are easily distinguishable by body shape and size. The sex of adult animals is readily apparent, although the sex of immature animals is difficult to determine with confidence. Most adult male capuchins exhibit distinctive scars, dark facial marks, broken or missing fingers, and/or piebaldism. Unique markings on individual animals and the groups' distinctive age/sex compositions enabled us to identify the same groups on subsequent encounters. All searching teams included at least one observer with extensive experience at individually identifying capuchins.

Table 2. Search effort, results, and population density estimates for *C. a. aequatorialis* at census localities.

Site (# search days)	Start Date	End Date	Hours ^a searched/ contact	# Contacts	Area (ha)	Pop. Density (Indiv/km ²)
Cabo Pasado (7)	7/06/02	7/14/02	68/0	Not present ^b	4000	-
Cerro Blanco Protected Forest (116)	7/10/04	4/15/05	688/85.1	40	2929	2.0 ^c
Cerro Seco Biological Reserve (2)	6/27/02	6/29/06	8/0	Not present ^b	40	-
Chirije (and vicinity) (4)	7/21/07	7/25/02	32/<1	1	240	-
Hacienda Paraíso (96)	7/01/03	12/01/03	620/13	11	2400	2.3
Jauneche (14)	7/14/04	7/28/04	240.9/36.4	55	138	22
La Hesperia Biological Reserve (10)	9/27/04	10/08/04	66/2.7	4	814	-
Lalo Loor Dry Forest Reserve (13)	9/06/04	9/21/04	77.3/6.7	5	200	2.5
San Isidro (forest fragments) (4)	7/01/02	7/05/02	60/0	Not present ^b	~800 total	-
Cordillera de Jama ^d	-	-	-	-	620	3.5
El Palmar ^d	-	-	-	-	950	3.9

^a Search hours multiplied by the number of observer groups searching simultaneously along separate routes.

^b After extensive censuses we concluded/confirmed that *C. a. a.* was not present at the site.

^c Includes solitary males encountered

^d Population density estimates from reference [11].

Home range characteristics and habitat selection

At one of our census sites, Cerro Blanco, we encountered groups frequently enough to investigate habitat preferences and home range characteristics. When encountered, groups often ran from the observers, and the areas that they use while fleeing may not represent the areas that they select for routine activities. Therefore, we included only the points at which the groups were first sighted for constructing home ranges and analyzing habitat selection. For the two groups that we encountered on at least 10 separate occasions, we calculated home ranges using kernel density estimation [23]. We used the *reference bandwidth* method in the R package *adehabitatHR* [24] to estimate the smoothing parameter. We used the 85% isopleth to delimit the home range boundary, following recommendations by Borger et al. [25]. Although these home ranges are based on a very small number of locations, kernel methods are robust to differences in sampling intensity, and they can provide accurate estimates of home range size with as few as 10 locations [25]. However, as we were unable to sample systematically, the home range estimates must be considered preliminary, and we urge caution in their interpretation.

To characterize the habitat at Cerro Blanco, we obtained or calculated raster data sets covering the extent of the reserve for the following variables: land cover, normalized difference vegetation index (NDVI), elevation, slope, distance to streams, distance to the boundary of the protected area, distance to roads (Table 3). NDVI is a measure of green vegetation based on the wavelengths of radiation characteristically reflected and absorbed by chlorophyll; therefore, NDVI values correlate strongly with the photosynthetic capacity of vegetation [26]. We produced maps of land cover and NDVI from a Landsat ETM+ image (Path 11, Row 61, 28.5 m resolution, 7 spectral bands) acquired November 23, 2000. We cropped the image around the approximate boundaries of the reserve, and we used unsupervised classification with the ISODATA clustering algorithm in PCI Geomatica 9.1 to partition the image into 30 land cover classes. We aggregated all non-forest classes into a single class, and we retained two forest classes that we labeled Mature Forest and Degraded Forest. We used a GeoEye-1 satellite image (resolution 1.65 meters) acquired November 25, 2009 in Google Earth to verify the accuracy of the classification. We applied a sieve filter to the classified image with a polygon threshold size of 9 pixels to remove small (<1 ha) habitat blocks within larger continuous areas of a different habitat type. We obtained the elevation data from the ASTER Global Digital Elevation Map. We calculated slope from the elevation data using the Spatial Analyst extension for ESRI ArcGIS 9.3. To obtain the final three distance variables, we manually traced streams, roads, and the protected area boundary using high-resolution imagery in Google Earth. We imported these features to ArcGIS 9.3, and used the Spatial Analyst extension to calculate the distance layers. We resampled all raster layers to 30 m cells using the nearest neighbor rule, adjusted grid cell alignment as needed, and clipped all seven data sets to the polygon formed by the boundary of the protected area (Fig. 2).

Table 3. Environmental variables used to assess habitat preferences of *C. a. aequatorialis* at Cerro Blanco Protected Forest, Ecuador.

Environmental Variable	Description	Study area values: mean (range)	Capuchin sighting values: mean (range)	Source
Land.Cover	Forest cover in 3 categories: non-forest (0), degraded (1), and mature (2)	(0 - 2)	(0 - 2)	Landsat 7 ETM+ ^a
NDVI	Measure of green vegetation	0.001 (-0.314 - 0.265)	0.058 (-0.129 - 0.174)	Landsat 7 ETM+ ^a
Elevation	Altitude above sea level	261 (29 - 409)	288 (149 - 391)	ASTER GDEM ^b
Slope	Degree of inclination of the ground surface to the horizontal	15.1 (0 - 55.1)	10.5 (2.2 - 22.5)	From Elevation
D.Streams	Distance to streams	228 (0 - 979)	93 (0 - 395)	Derived from vector layer of streams
D.Roads	Distance to dirt roads	439 (0 - 1549)	296 (0 - 1046)	Derived from vector layer of roads
D.Boundary	Distance to boundary of the protected area	633 (0 - 1838)	916 (31 - 1800)	Derived from vector layer of protected area boundary

^a Downloaded from <http://glovis.usgs.gov/>; ^b ASTER GDEM is a product of METI and NASA. Downloaded from <http://www.gdem.aster.ersdac.or.jp/>

We used the R package adehabitat HS [24] to analyze habitat selection using Mahalanobis Distances factor analysis [27,28]. This analysis makes use of the niche concept [29], in which each of several environmental variables defines one dimension of the organism's "ecological space." It is assumed that the study area consists of discrete resource units (e.g. pixels of a raster map) on which a set of environmental variables have been measured. The goal of the method is to identify the differences between the availability and use of these resource units, and to relate the difference with directions in the principal components of the ecological space. We used the seven environmental variables described above for the analysis, and since we were interested only in habitat use and availability at the population level, we pooled all of the locations at which capuchins were first sighted (including solitary animals and unidentified groups, $N_{\text{total}} = 31$). For the categorical land cover data set, we calculated Manly resource selection ratios [30] for each of the land cover classes using the R package adehabitatHS. These ratios are measures of use versus availability for each land cover class. We evaluated the significance of selection for land cover with log-likelihood χ^2 tests. Because all of the habitat selection analyses described here are based on a small number of locations with nonuniform sampling effort and detection probability, the results must be considered exploratory. While we made every effort to search the study site as systematically as possible, in our analyses we were unable to control for any bias that resulted from searching the resource units unequally.

Research complied with protocols approved by the Appalachian State and Tulane University IACUCs, and adhered to the legal requirements of Ecuador and the United States.

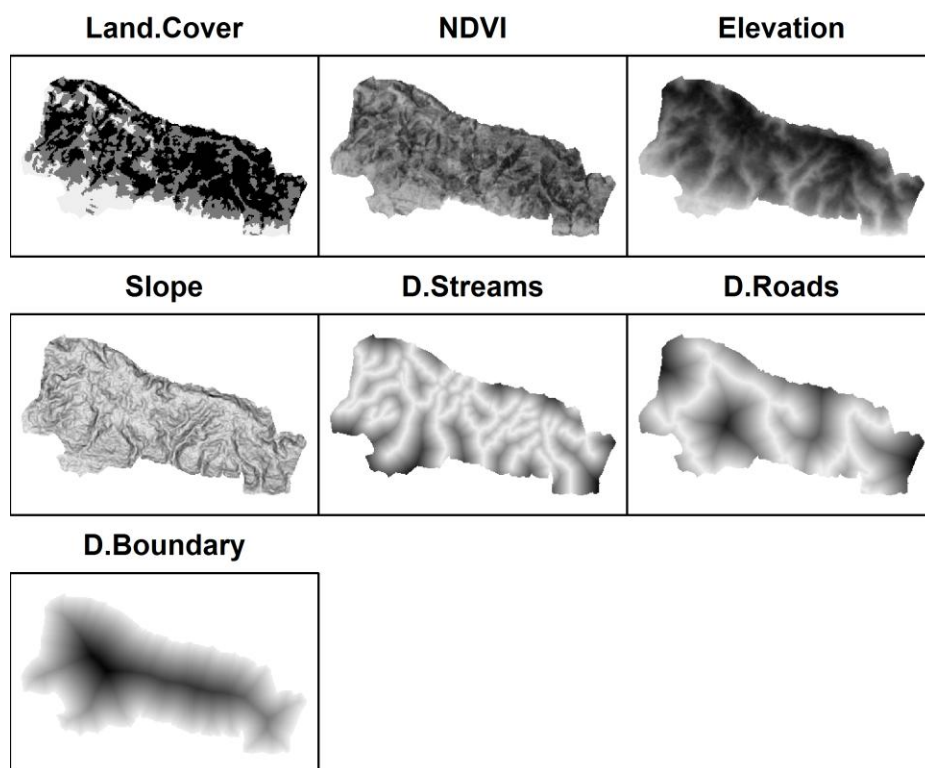


Fig. 2 Maps of the seven environmental variables used for the habitat selection analysis at Cerro Blanco. Values of the variables increase from light to dark gray.

Results

Survey results and geographic limits

We confirmed the presence of *C. a. aequatorialis* at 7 of 11 sites that we surveyed, including four new presence localities for which no previous published record exists (Table 1). Two of the surveyed sites, San Isidro and Cerro Seco Biological Reserve, were too young and/or fragmented to support capuchins, although mantled howler monkeys (*Alouatta palliata*) were present at San Isidro. We did not encounter capuchins during the week that we spent intensively searching the unprotected site Cabo Pasado, although this large fragment supports a healthy population of *A. palliata* (note: two additional two week long field schools were run at this site in 2002 and 2003, and no capuchins were ever observed). Informants reported to us that *C. a. aequatorialis* occurred at this site in the recent past, but they have not been observed since approximately 1998, suggesting local extinction. Our brief surveys and interviews did not reveal evidence of *C. a. aequatorialis* in Cotacachi-Cayapas, although Tirira [9] lists it as present here. Other published data [31] indicate that Cotacachi-Cayapas is also inhabited by *C. capucinus*. Local guides near the village of San Miguel, located at the southern edge of the park, confirmed to us that *C. capucinus* was present, but none reported having seen *C. a. aequatorialis* in the area. There was only one site, Manglares Churute, at which local informants indicated that *C. a. aequatorialis* was present but we were not able to confirm the reports visually.

Table 4. Compositions of groups^a of *Cebus albifrons aequatorialis* encountered during this study. AM: Adult male, AF: Adult female, SAM: Subadult male, JUV: Juvenile, INF: Infant, UNK: Unknown, IMM: Immature (Juvenile + Infant).

Group	Site	AM	AF	SAM	JUV	INF	UNK	Total	AM:AF ratio	IMM:AF ratio
1	Cerro Blanco Protected Forest	6	5	4	4	1	0	20	1.20	1.00
2	Cerro Blanco Protected Forest	2	3	2	2	1	0	10	0.67	1.00
3	Cerro Blanco Protected Forest	3	2	4	6	1	2	18	1.50	3.50
4	Hacienda Paraíso	1	3	3	1	2	4	14	0.33	1.00
5	Hacienda Paraíso	1	1	0	1	1	9	13	1.00	2.00
6	Hacienda Paraíso	3	2	0	3	2	5	15	1.50	2.50
7	Hacienda Paraíso	2	2	0	1	1	6	12	1.00	1.00
8	Jauneche	2	5	3	6	4	0	20	0.40	2.00
9	Jauneche	2	4	3	3	1	0	13	0.50	1.00
10	La Hesperia Biological Reserve	1	4	2	4	2	0	13	0.25	1.50
11	Lalo Loor Dry Forest Reserve	2	3	0	0	0	0	5	0.67	0.00

^a Does not include solitary individuals encountered

Intensive censuses, demography, and population density estimates

Between July 2003 and April 2005, we encountered *C. a. aequatorialis* groups a total of 115 times during 1,692 search hours at six sites (Table 2). Search effort, contact hours, and population density estimates are summarized for each site in Table 2. Population densities ranged from 2.0 to 22.0 individuals/km² (median = 2.4 individuals/km²). We did not estimate population densities for two sites at which we encountered capuchins—Chirije and La Hesperia—because we consider our censuses at these sites inadequate for the complete-count census method. At Chirije we obtained a poor count during our only capuchin encounter at

this site. At La Hesperia, the steep terrain and lack of an extensive trail system prevented us searching in a systematic manner. Table 4 summarizes the sizes and age/sex compositions of each of the groups that we encountered. Mean group size was 13.9 individuals (range 5 – 20), and most groups included multiple adult males and adult females. Among adults, there was a slight bias towards females, with 0.82 males for each female. However, if we include the subadult males, then males outnumber females markedly (ratio = 1.39). The mean immature (juvenile + infant) to adult female ratio was 1.5, and immatures were at least as numerous as adult females in all encountered groups except for one (Lalo Loor).

Behavioral observations

All of the capuchin groups that we encountered responded to our presence with intense vigilance, observer-directed alarm calls, and avoidance. Although we had intended to investigate daily activity patterns, the monkeys that we encountered spent nearly all of their time either threatening or fleeing from us. The fear responses were most acute at Hacienda Paraíso, Lalo Loor, and Jauneche. Capuchins at these sites fled immediately and sometimes split into subgroups as they ran off. At Lalo Loor and Jauneche, we observed monkeys using agricultural areas adjacent to the reserves, including plantations of banana, corn, plantain, and cacao, and informants at both sites indicated that the capuchins had been harassed by the crop owners. At Cerro Blanco, we observed capuchins eating a variety of foods including insects, the tender bases of epiphytic bromeliad leaves, and the fruits of *Vitex gigantica*, *Spondias* sp., *Eugenia* sp., *Ficus* sp., and *Cecropia* sp.

Home ranges and resource selection

We encountered two capuchin groups at Cerro Blanco frequently enough to calculate home range sizes and investigate habitat selection. The Candil group's home range based on 11 encounters totaled 561 ha, while the Cuzumbo group's home range area based on 10 encounters encompassed 507 ha (Fig. 3). A visual comparison of the distributions of available resource units versus used resource units for each habitat variable suggests selection for areas with mature forest, high elevation, low slope, and high NDVI that are located near streams, near roads, and far from the boundary of the protected area (Fig. 4). The Mahalanobis Distances factor analysis revealed strong negative selection along the first factorial axis and weak negative selection along the second factorial axis (Appendix 1).

The first factorial axis shows strong positive correlation with distance to streams and strong negative correlation with NDVI, elevation, and forest cover; it also shows weaker positive correlation with slope and negative correlation with distance to the boundary (Appendix 2). The observed negative selection along this axis therefore indicates preference for relatively flat, high-elevation, well-forested, semi-evergreen areas close to streams and far from the boundary. The second factorial axis has a strong positive correlation with distance to roads, a weaker positive correlation with elevation, and a weak negative correlation with NDVI. The observed negative selection along this axis therefore indicates preference for semi-evergreen, low-elevation areas near roads. Selection for land cover was significant ($\chi^2 = 6.684$, $df = 2$, $p = 0.0354$) overall. Capuchins showed significant selection against non-forest (proportion used = 0.032, proportion available = 0.160, $SE = 0.202$, selection ratio = 0.199, $p < 0.001$). Selection for mature forest approached significance (proportion used = 0.613, proportion available = 0.442, $SE = 1.387$, selection ratio = 0.198, $p = 0.051$), while there was no apparent selection for or against areas with degraded forest (proportion used = 0.355, proportion available = 0.398, $SE = 0.891$, selection ratio = 0.1990.216, $p = 0.613$).

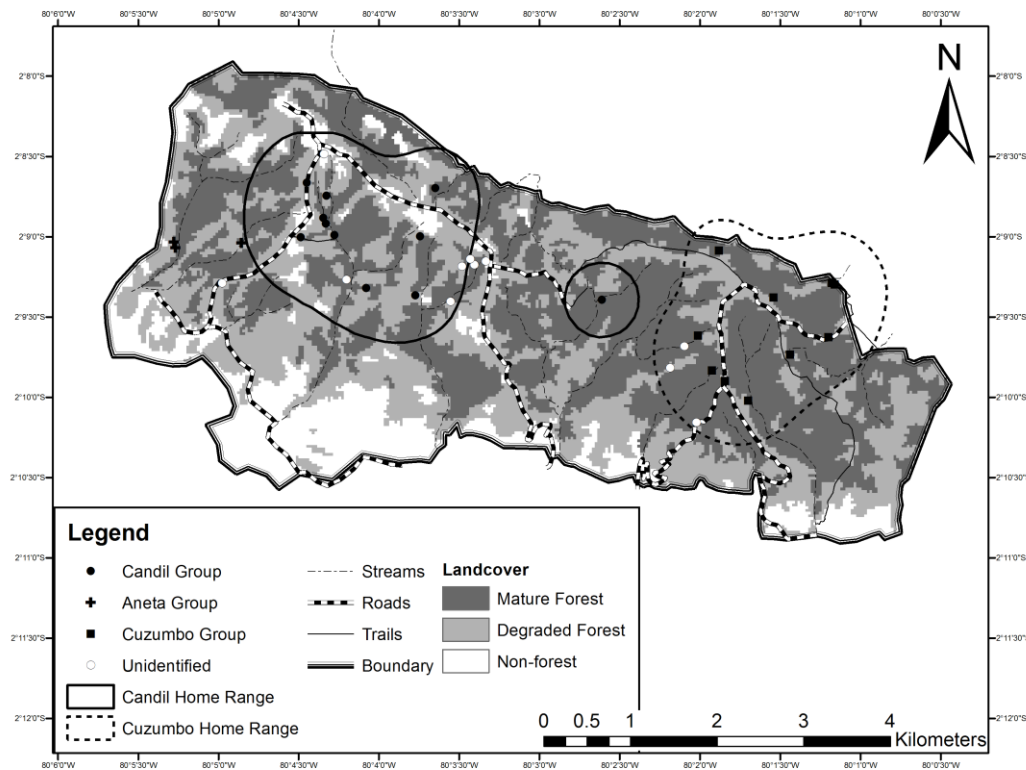


Fig. 3 Map of *Cebus albifrons aequatorialis* sightings, land cover, and landscape features at Cerro Blanco. Kernel density estimations of home ranges for two groups are also shown. The Cuzumbo group's home range extended outside of the protected area along streams containing degraded forest

Discussion

New presence localities

During our censuses and surveys, we found four previously undocumented populations of *C. a. aequatorialis* in the small, private reserves/haciendas of Chirije, Hacienda Paraíso, La Hesperia, and Lalo Loor. These data together with those of other researchers [11-13,17,18,32], show that *C. a. aequatorialis* populations exist in at least 20 forested areas in western Ecuador and northern Peru. While these additional presence localities are encouraging, we emphasize that the long-term survival prospects of this subspecies remain uncertain [16], as several of these areas are not officially protected, and hunting and deforestation are problematic even in protected areas.

Geographic range

There are numerous sites north of the Esmeraldas-Guayllabamba River at which *C. capucinus* is reported present [17,31,33], but to our knowledge there are no reports of *C. a. aequatorialis* north of this large river except for one: Tirira [9] states that *C. a. aequatorialis* occurs in Cotacachi-Cayapas Ecological Reserve. *C. a. aequatorialis* is reportedly absent from buffering protected forests that are adjacent to the south of Cotacachi-Cayapas, including the Los Cedros Biological Reserve [33] and the Awa Indigenous Reserve [34]. In addition, Tirira [34] considers the Esmeraldas-Guayllabamba River to be the southern limit of *C. capucinus* in Ecuador. Thus, the Esmeraldas-Guayllabamba River is likely to be the northern limit of the geographic range of *C. a. aequatorialis*, although there may be an isolated population north of the river in Cotacachi-Cayapas. Aside from this locality, the northernmost site inhabited by *C. a. aequatorialis* is Bilsa Biological Station (0.360° N, 79.700° W, locality 1 in Fig. 1) in Mache-Chindul National Park, Esmeraldas province, Ecuador [32]. The easternmost inhabited site is La Hesperia (0.367° S, 78.870° W, Fig. 1), which is located in the western Andean

foothills of Ecuador at an altitude between 1100 and 2040 m, between the cities of Machachi and Santo Domingo de los Colorados. To our knowledge, La Hesperia also represents the highest altitude currently inhabited by this subspecies, although Allen [5] notes that a specimen, presumably of *C. a. aequatorialis*, was collected at 1,660 m in Gualea, Ecuador. In Ecuador, we confirmed the presence of *C. a. aequatorialis* as far south as Manglares-Churute (2.412° S, 79.634° W, Fig. 1), and Albuja and Arcos [11] list additional inhabited sites in the far south of Ecuador. The southernmost inhabited site is Cerros de Amotape National Park (4.136°S, 80.588°W, locality 13 in Fig. 1) [12] in northern Peru.

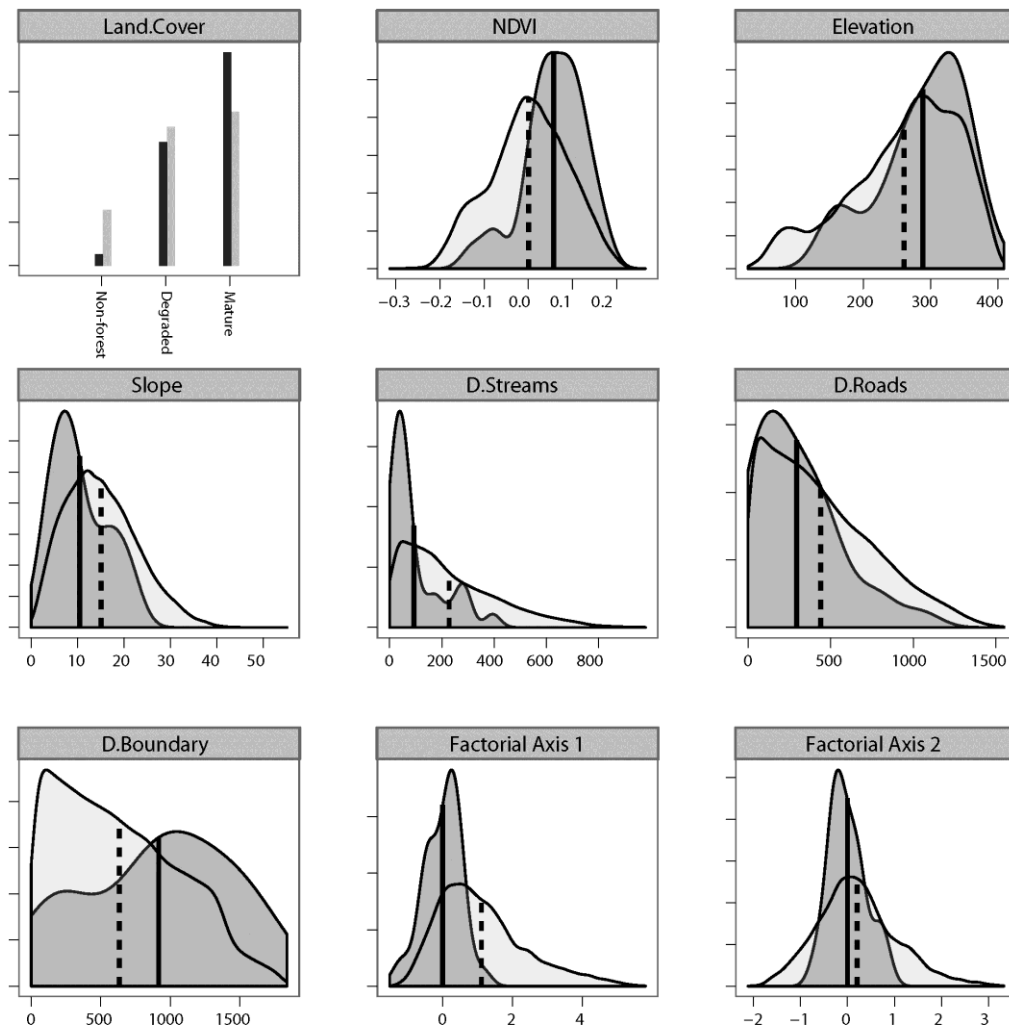


Fig. 4 Comparison of distributions of available (light gray) versus utilized (dark gray) resource units measured for the seven habitat variables. Distributions for the continuous habitat variables are smoothed using kernel density estimation, and the distribution for the categorical variable land cover is represented as a histogram with Non-forest on the left, Degraded Forest in the middle, and Mature Forest on the right. The last two plots show the distribution of available and used resource units along the first and second factorial axes of the Mahalanobis Distances factor analysis. Solid lines indicate means of the used distributions, and dashed lines indicate the means of the available distributions.

Demographic characteristics

C. a. aequatorialis live predominantly in multi-male multi-female social groups, as in all other well-studied *Cebus* taxa. We calculated a mean group size of 13.9 across all groups and sites, which accords well with those previously reported for this subspecies [11,13,17,18]. Given the poor level of habituation of all the monkeys we observed, it is possible that some of our group counts were incomplete, although they correspond well with those reported for other subspecies of *C. albifrons* [references 35-37, but see 38]. This value also falls within the range of observed mean group sizes for other *Cebus* taxa at established research sites, though near the lower limit [table 4.2a in 39].

Excluding the extreme outlier Jauneche, and including two sites (Cordillera de Jama and El Palmar) censused by Albuja and Arcos [11], the mean population density for *C. a. aequatorialis* across five sites with reliable estimates is 2.8 individuals/km² (range: 2.0 – 3.9). These densities are considerably lower than the population densities recorded for other subspecies of *C. albifrons*: 24 individuals/km² for *unicolor* in Peru [36], 13.5 individuals/km² for *trinitatis* in Trinidad [37], 7.8 - 46 individuals/km² for *albifrons* in Brazil [40,44] and 15.8 individuals/km² for *albifrons* in Colombia [41]. The five sites with low population densities for *C. a. aequatorialis* consist of tropical dry forest with high rainfall seasonality, whereas most of the population densities for other *C. albifrons* populations are from sites with higher rainfall and less seasonality. Thus, *C. a. aequatorialis* may occur at low population densities because fruit abundance in the dry areas that they inhabit is likely lower overall and less predictable than in rainforests. The outlier in our dataset, Jauneche, is a 138-ha forest fragment that consists of mature moist forest. We believe that the density of *C. a. aequatorialis* is unusually high at Jauneche because the monkeys routinely raid the crops in surrounding plantain, corn, and cacao plantations, and the fragment is completely isolated.

The composition of the *C. a. aequatorialis* groups that we observed, with a sex ratio of 0.82 adult males for each adult female, also closely match those of other studied *Cebus* populations [average ratio for the genus: 0.81, from table 4.2b in 39]. Including the subadult males in this calculation results in a higher male to female ratio (1.39) that is more similar to *C. a. unicolor* at Cocha Cashu, Peru [36,42]. The relatively high immature to adult female ratio (1.5) suggests good reproductive and survival rates [43]. The overall picture of *C. a. aequatorialis* grouping patterns that emerges from our observations fits the typical *Cebus* pattern.

Home range characteristics and habitat selection

Although the data are preliminary, our home range estimates for two groups in Cerro Blanco (561 ha and 507 ha) are considerably larger than home range sizes reported for other untufted capuchins: 150 ha for *C. albifrons* in Peru [36], 120 ha for *C. albifrons* in Colombia [38], 275 ha for *C. olivaceus* in Venezuela [44], 133 - 237 ha for *C. capucinus* in Costa Rica [Campos, Childers, and Parr unpublished data]. Cross-study comparisons of home range size are complicated by the use of different analytical methods, and it is possible that home range sizes in our analysis were inflated because our very low sample size resulted in over-smoothing the kernel density estimations. However, we have the impression that *C. a. aequatorialis* at Cerro Blanco does indeed occupy unusually large home ranges. For example, we found the Candil group in four different valley systems, with a straight-line distance of nearly 4 km between the two most widely separated sighting locations. The extremely low population density at which *C. a. aequatorialis* exists across its geographic range supports our finding that home ranges in this subspecies may be unusually large for *Cebus*. Data on *C. a. aequatorialis* home ranges from additional sites are clearly needed to confirm this finding.

As expected, our analysis of habitat selection at Cerro Blanco revealed a significant preference for forest habitat types over non-forest, but interestingly the capuchins did not exhibit selection for or against areas with degraded forest. Although preliminary, this result suggests that *C. a. aequatorialis* can successfully exploit disturbed and secondary forest, which may contain a different set of food resources than those found in undisturbed forest. Similarly *C. capucinus* in a Costa Rican dry forest routinely forage in both mature and degraded forest areas [45,46]. We observed strong positive selection for proximity to streams and roads. These results are likely due in part to selection bias, as streams and especially roads were the areas that we were able to search most effectively. However, *C. capucinus* in Costa Rica also show strong preference for proximity to water sources [47,48], and their population densities appear to be limited by access to water [49]. We also observed positive selection for areas with higher NDVI; that is, for greener areas. It is likely that these areas provide greater food abundance for primates, as in South African vervet monkeys [50]. Finally, capuchins selected weakly for higher elevation and against proximity to the boundary of the protected area. These findings are likely due to the park's hilly topography, with more densely forested areas in the higher-elevation center of the reserve and degraded or non-forested areas around the park periphery. In addition, capuchins may have avoided the park's boundaries due to increased hunting pressure in these areas.

Implications for conservation

The sites inhabited by *C. a. aequatorialis* range from dry forest near sea level to wet pre-montane Andean forest. We observed monkeys in both mature primary forest and highly disturbed areas consisting of mixed secondary forest and cultivation (Fig. 5). Because *C. a. aequatorialis* is clearly capable of exploiting a highly varied range of foods and habitats, we believe that if effective protection can be established, there is good potential for these small, fragmented populations to grow and expand into regenerating areas. As an example, the population of *C. capucinus* in northwestern Costa Rica has grown steadily in regenerating forest since the establishment of the Area de Conservación Guanacaste from reclaimed ranchlands [49,51-53]. Our finding that *C. a. aequatorialis* uses degraded forest roughly in proportion to its abundance underscores the importance of conserving not only less-disturbed “core” areas of forest that remain in western Ecuador, but also the surrounding degraded and secondary forest areas.



Fig. 5. Adult female (left) and juvenile *Cebus albifrons aequatorialis* in the tropical dry forests of Cerro Blanco. Photos by Fernando Campos.

We lack data to evaluate population trends at most inhabited sites for *C. a. aequatorialis*, but Parker and Carr's [17] census at Jauneche provides an opportunity for comparison. Parker and Carr [17] reported seeing four distinct social groups of capuchins ranging in size from 5-18 individuals, with a total population of 37 individuals. In our census 13 years later, the total population at Jauneche consisted of 33 individuals in two social groups ranging in size from 13-20. These data suggest that the Jauneche population is approximately stable or decreasing slightly, with significant restructuring of the social groups. Further study is needed to determine if the lack of population growth is due to high mortality or high rates of emigration relative to immigration. Inbreeding depression is also a possibility at this small and highly isolated forest fragment.

In western Ecuador, decades of deforestation accompanied by rapid human population growth have eliminated most large tracts of forest [15]. Although many of the sites where we confirmed the presence of, *C. a. aequatorialis* have been set aside as protected areas, forest conversion still occurs within their boundaries. Aside from habitat loss, *C. a. aequatorialis* are threatened by hunting for bushmeat and the pet trade, and in some areas they are harassed/killed by farmers whose crops the monkeys raid [12; personal observations]. Although these threats remain grave, the several heartening developments in the last decade bode well for *C. a. aequatorialis* conservation. The Critical Ecosystem Partnership Fund and Conservation International have invested heavily in promoting conservation corridors among forest patches in the Chocó-Manabí region. At the governmental level, the recently implemented Programa Socio Bosque, whereby the Ecuadorian government provides monetary incentives to farmers and indigenous communities who commit to protect their forests, is tremendously encouraging. Furthermore, private NGOs dedicated to the conservation of forests in western Ecuador, including Fundación Jatun Sacha, Fundación Pro-Bosque, and Fundación Ceiba, have put conservation measures into action at several sites inhabited by *C. a. aequatorialis*, and their continued actions will surely prove instrumental for the continued survival of this highly endangered primate.

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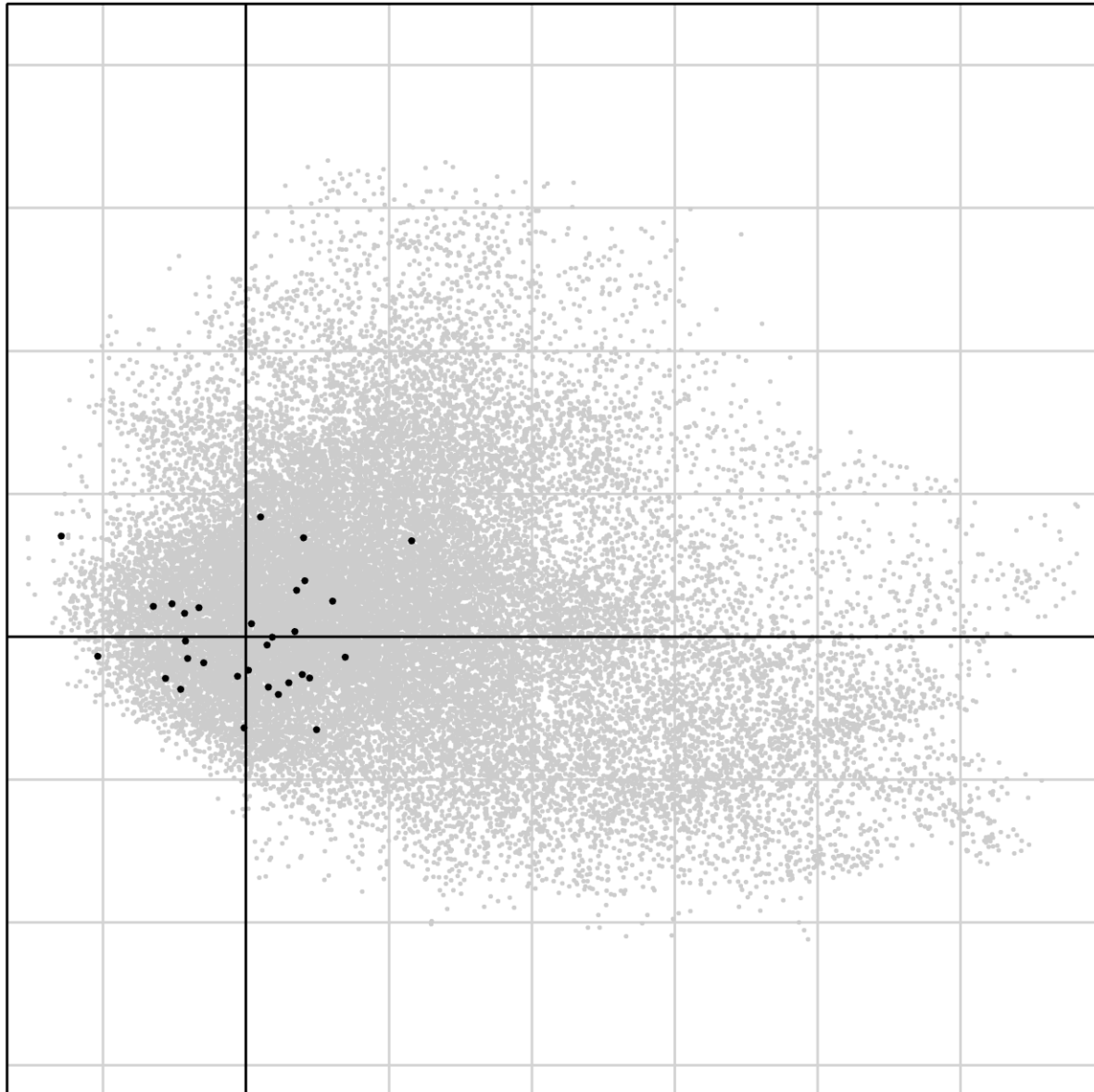
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Appendix 1. Available (gray) and utilized (black) resource units in the multidimensional space defined by the seven habitat variables, plotted here on the first factorial plane found by the Mahalanobis Distances factor analysis. The utilized niche is centered on the origin by definition. Relative to the used niche, the available ecological space is strongly skewed toward positive values on the first factorial axis (x-axis) and weakly skewed toward positive values on the second factorial axis (y-axis).



Appendix 2. Diagram indicating strength and direction of correlations between the seven environmental variables and the first (x-axis) and second (y-axis) factorial axes. The first factorial axis shows strong positive correlation with distance to streams and strong negative correlation with NDVI, elevation, and land cover. The second factorial axis shows strong positive correlation with distance to roads.

