Completeness of rapid assessments of medium and large mammal diversity in the northwestern Amazon in Colombia

Darwin M. MORALES-MARTÍNEZ1*, Natalia ATUESTA-DIMIAN1, Daniela MARTÍNEZ-MEDINA2, Diego R. GUTIÉRREZ-SANABRIA3, Miguel E. RODRÍGUEZ-POSADA2

1 Instituto Amazónico de Investigaciones Científicas SINCHI, Programa Ecosistemas y Recursos Naturales, Grupo de Investigación Fauna Amazónica Colombiana, Bogotá, Colombia
2 Fundación Reserva Natural La Palmita, Centro de Investigación, Grupo de investigación territorial para el uso y conservación de la biodiversidad, Bogotá, Colombia
3 Universidad de Pamplona, Grupo de Investigación en Ecología y Biogeografía, Pamplona, Colombia
* Corresponding author: drmoralesmar@gmail.com; https://orcid.org/0000-0001-5786-4107

ABSTRACT
Rapid assessments are the most common information source on biodiversity in the northwestern Amazon in Colombia due to limited resources and logistic constraints. These assessments are essential for decision-making on environmental policies in this region, that has been strongly impacted by the transformation of its natural ecosystems. Several local camera-trapping rapid assessments of medium and large-sized mammals (MLM) have been conducted in the Colombian Amazon, but they are difficult to compare. We analyzed information of 16 of these rapid assessments of MLM to provide the first list of MLM in the northwestern Amazon in Colombia. We also evaluated the accuracy of four estimators (ICE, Chao-2, Jackknife-1, and Jackknife-2), and the minimum sampling effort for the estimation of MLM richness in local surveys in the region. We report 26 species of MLM for the Colombian Amazon (between five and 13 species per locality), which is an underestimation of MLM richness in the region. The best estimator of MLM richness was the Jackknife-1, due to its precision and the lower influence of singletons. We recommend a minimum sampling effort of 350 camera trap-days. Although rapid assessments do not allow a robust estimation of MLM richness, they record the most common species (or core species) per locality and their abundance variation. The evaluation of the effect of habitat transformation on MLM and the estimation of population parameters of rare species require more intensive studies.

KEYWORDS: camera trapping, neotropics, rainforest, sampling effort, satellite species, species richness

Completeness de inventarios rápidos de diversidad de mamíferos medianos y grandes en la Amazonía noroccidental colombiana

RESUMEN
Las evaluaciones rápidas de biodiversidad son la fuente de información más común sobre biodiversidad en el noroccidente amazónico en Colombia debido a que los recursos y la logística son limitados. Estas evaluaciones son esenciales para tomar decisiones ambientales en esta área que ha sido impactada por la transformación de sus ecosistemas naturales. Diferentes evaluaciones locales rápidas con cámaras trampa de mamíferos medianos y grandes (MMG) se han realizado en el noroccidente Amazónico en Colombia, pero estas son difícilmente comparables. Nosotros recolectamos la información de 16 evaluaciones rápidas de MMG para proporcionar la primera lista de MMG del noroccidente amazónico en Colombia. Adicionalmente, evaluamos la precisión de cuatro estimadores (ICE, Chao 2, Jackknife 1 y Jackknife 2) y el esfuerzo mínimo de muestreo para la estimación de la riqueza de MMG en estudios locales en esa región. Reportamos 26 especies de MMG para la Amazonía colombiana (entre cinco y 13 especies por localidad), lo que es un subestimación de la riqueza de MMG en la región. El mejor estimador para este tipo de estudios fue Jackknife 1, debido a su precisión y la baja influencia de singletons. Recomendamos un esfuerzo mínimo de muestreo de 350 cámaras trampa-día. Aunque las evaluaciones rápidas no proveen una estimación robusta de la riqueza de MMG, estas evaluaciones registran las especies más comunes (especies core) y la variación en su abundancia por localidad. Es necesario un mayor esfuerzo de muestreo para evaluar el efecto de la transformación del hábitat sobre los MMG, en especial sobre los parámetros poblacionales de las especies raras.

PALABRAS CLAVE: esfuerzo de muestreo, especies satélite, neótrópico, selva húmeda tropical, trampas cámara, riqueza de especies

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INTRODUCTION

The Colombian Amazon, comprising the northwestern area of the Amazonian biome, is environmentally heterogeneous and recognized for its exceptional biodiversity of mammals (Rodríguez-Mahecha et al. 2006). Ironically, this biodiversity has been poorly studied, and the region remains vastly scientifically unexplored (Stevenson et al. 2004; Montenegro 2017; Trujillo et al. 2019), while at the same time being submitted to intense and accelerated ecosystem transformation that involves the highest fire frequencies (Otavo and Murcia 2018) and up to 76% of the total deforestation rate (IDEAM 2020) in Colombia. After the Colombian peace process in 2016, deforestation rates increased between 46% and 346% within protected areas of the Amazon region (Clerici et al. 2020). In this scenario of few studies and high impact, it is urgent to increase the knowledge on biodiversity in the Colombian Amazon, to better understand how different taxonomic groups respond to human pressure, and to provide information for sound environmental and conservation decisions (Boron et al. 2019).

Medium and large mammals are key species in neotropical ecosystems because they control plant and animal populations, acting as predators and herbivores, long-distance seed dispersers (Árêvalo-Sandi et al. 2018) and pathogen reservoirs (Mollentze and Streicker 2020), among other functions. These mammals also contribute significantly to food security in several indigenous communities (Osorno et al. 2014) but are sensitive to habitat changes and overexploitation (Romero-Muñoz et al. 2020) and populations of many species are in decline (Benitez-López et al. 2019).

To assess the diversity of Colombian Amazon fauna and its use by the native communities, the Instituto Amazónico de Investigaciones Científicas SINCHI has been doing local camera-trap rapid assessments throughout the Colombian Amazon since 2014. Due to economic and logistic constraints, most of these assessments are short-term and differ substantially in sampling effort, making them difficult to compare. Despite this handicap, these inventories accumulate valuable information on medium and large mammal richness in the region. Species richness is the most frequent parameter used to describe communities, being vital for the analysis of species distributions, assessment of human perturbation, and conservation planning (Pineda-López 2019). Albeit providing only crude estimates, these rapid assessments give a general picture of local mammal assemblage composition, mostly on core species – locally abundant and regionally common species – and some satellite species – species that are sparse and occur at only a few sites with low abundance (Hanski 1982).

Here we aimed to evaluate data on several rapid camera-trap surveys to provide the first comprehensive assessment of the diversity of medium and large mammals in the northwestern Amazon in Colombia, and to assess the effectiveness of these surveys to record core and satellite species. We also used the data to determine which of several estimators provides the most precise estimation of species richness and recommend a minimum sampling-effort to estimate species richness of medium and large mammals for future studies in the region.

MATERIAL AND METHODS

Study area

The Colombian Amazon comprises the northwestern extreme of the Amazon biome and includes an area of approximately 477,274 km², representing 42% of the Colombian continental area. This region extends from the eastern slopes of the Andes to the border with Venezuela, Brazil, Peru and Ecuador, and to the forest line north of the Guaviare River (Murcia et al. 2007; Figure 1).

The northwestern Amazon is a heterogenic region mainly covered by tropical rainforests. It includes two biogeographic provinces [Amazonas and Guyana (sensu Hernández-Camacho et al. 1992) or Imerí and Napo (sensu Morrone 2014)], and at least eleven biogeographic districts (sensu Hernández-Camacho et al. 1992). The mean annual temperature is cooler near the Andes (24.3–25.4 ºC) and increases towards the northeastern edge of the region (26.2–27.9 ºC) (Rudas 2009). The precipitation is higher in the Andean foothills (5,400 mm annual rainfall), and decreasing eastwards, with the lowest record in the northeastern portion (2,200 mm), and the highest lowland precipitation records in the south between 2°N and 4°S (3,300–3,900 mm) (Rudas 2009).

Camera-trap sampling data

We used local rapid assessment information on medium and large mammals (MLM) from 16 localities obtained...
by the SINCHI Institute (Figure 1) in five departments (Caquetá, Guaviare, Guainía, Vaupés, and Vichada), between the Guaviare-River forest (transitional jungles between the Amazonas and the Orinoco Llanos regions) to the north, and the Caquetá River to the south. The distance between localities varies from 20 km to 928 km. The overall survey area comprises ten ecosystems and several vegetation types such as the cloud forest of the Andean foothills, lowland floodplain and terra-firme forest, and natural Amazonian savannas.

The sampling effort of the rapid assessments varied from 60 to 241 camera trap-days (the sum of days during which each camera remained active at a locality) (Table 1). The samplings did not have a specific design, but they had similar parameters: 1) between 7 and 20 cameras were installed at 0.5 to 1 km distance among them, and therefore did not cover areas larger than 15 km²; 2) cameras were set at 40 cm above the ground and programmed to take three pictures per trigger with intervals of one second between photos; 3) cameras ran 24 hours per day, recording the date and time of each photograph; 4) no bait was used to attract mammals; 5) cameras were installed close to track signals, salt licks, and feeding sites to increase capture probability; and 6) in nine surveys, the cameras were placed in the same geographic location through the complete sampling window, while in seven surveys some or all cameras were placed in one locations for a few days and then were changed to different locations. Each geographic location was considered as a different station.

Our analyses focused on terrestrial mammals with a weight greater than 2 kg, thus we excluded primates and other mainly arboreal mammals seldom captured on camera traps. Rats and mice that may exceed 2 kg (e.g., Proechymis) were also excluded because they cannot be identified without a voucher specimen with a clean skull (Voss and Emmons 1996). We based the taxonomic treatment of medium and large mammals on Ramírez-Chaves et al. (2019).

Records of a species at the same site were considered as independent events when the photographs were separated by at least one hour, to avoid pseudoreplication in the species counts (O’Brien et al. 2003; Srbek-Araujo and Chiarello 2013). We used the detection frequency (or catch per unit effort) to calculate a relative abundance index. The index was calculated as the number of independent photographs per species/camera trap-days * 100. Measuring abundance in this way allowed us to evaluate the commonness or rarity of each species. Given the difficulty in identifying individuals on camera-trap images, this measure does not represent the abundance or density sensu stricto (Magurran and Henderson 2011; O’Brien 2011). We classified the recorded species in a dichotomous category as core and satellite species sensu Hanski (1982). Core species include the most abundant species that were present in most of the rapid inventories (70% of all inventories). All species that occurred at only a few sites and in low abundance) were classified as satellite species.

### Sampling completeness and species richness estimation

Sampling completeness was measured at each locality based on the number of independent events using species-accumulation curves and the evaluation of four non-parametric estimators for species richness: ICE, Chao 2, Jackknife 1 (Jack 1), Jackknife 2 (Jack 2) using Estimates 9.0 (Colwell 2013). The completeness of each survey was calculated based on the ratio between observed richness and the total estimated richness. To estimate the species richness and the sampling completeness of each surveyed locality, we used each independent event as a sampling unit (Willott 2001). We based our analyses on the incidence data and randomized the shuffling between samples with 1000 iterations to avoid the order of appearance in the estimation (Soberón and Llorente 1993).

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**Table 1.** Metadata of camera-trap rapid assessments in 16 localities in the Colombian Amazon. N cameras = number of cameras used in the survey; N stations = number of different sites where cameras were placed during the sampling window; Sampling window = total number of sampling days of the survey; N camera trap-days = total sampling effort defined as the sum of the days that each camera trap kept active in the sampling window.

| Locality       | Geographic location | N cameras | N stations | Sampling window (days) | N camera trap-days |
|----------------|---------------------|-----------|------------|------------------------|-------------------|
| Andakí         | 1°40.232’N, 75°54.301’W | 20        | 67         | 13                     | 241               |
| Buenos Aires   | 0°2.308’S, 70°56.693’W | 19        | 19         | 7                      | 103               |
| Calamar        | 2°23.356’N, 72°41.143’W | 13        | 14         | 9                      | 117               |
| Carrajal       | 3°58.272’N, 68°9.227’W | 15        | 15         | 6                      | 75                |
| Cerro Campaña  | 1°17.060’N, 72°07.000’W | 18        | 18         | 5                      | 80                |
| El Retorno     | 2°13.882’N, 72°29.810’W | 14        | 19         | 11                     | 154               |
| Itilla         | 1°59.293’N, 72°53.424’W | 15        | 15         | 8                      | 64                |
| Lindosa        | 2°33.942’N, 72°53.294’W | 18        | 18         | 9                      | 121               |
| Matavén        | 4°28.786’N, 68°2.598’W | 20        | 30         | 14                     | 226               |
| Río Yari       | 1°56.980’N, 74°15.523’W | 16        | 16         | 9                      | 130               |
| Sabanas del Yari | 1°40.198’N, 74°11.395’W | 9         | 9          | 8                      | 60                |
| San José       | 2°24.171’N, 72°26.359’W | 14        | 19         | 13                     | 180               |
| Sejal          | 3°54.922’N, 68°18.375’W | 14        | 14         | 8                      | 88                |
| Tiquié         | 0°15.302’N, 70°6.158’W | 7         | 7          | 25                     | 175               |
| Tumia          | 1°40.422’N, 73°34.460’W | 20        | 20         | 6                      | 81                |
| Yavaraté       | 0°56.587’N, 69°13.127’W | 16        | 31         | 11                     | 111               |
| Tiquié (long term) | 0°15.303’N, 70°6.164’W | 22        | 102        | One year               | 211               |
To determine the least biased method to estimate species richness, we compared the four richness estimators by looking at: 1) the accuracy of the richness estimation; 2) the best fit between observed and estimated richness; and 3) which estimator is least affected by the influence of singletons (species with only one independent record in the sample). We assessed the accuracy of the estimators using the data for the locality of Tiquié (Figure 1). For this locality, we had long-term data for a whole-year survey (2111 camera trap-days) which we assumed to be a representative inventory of MLM as defined in this study. We compared the species richness resulting from the long-term data with the richness obtained with each estimator for the first sampling occasion at Tiquié (175 camera trap-days; Table 1). We used Pearson correlation to test the best fit of estimated and observed richness in all rapid assessments. To determine the influence of singletons, we performed a Pearson correlation between the estimated richness and the singletons. The significance level was p < 0.05.

**Minimum sampling effort**

We assessed the minimum sampling effort to reach a representative species richness for MLM in camera-trap assessments in the Colombian Amazon. We employed general linear models (GLM) using Poisson distribution (counts) to assess the effect of the sampling effort on the richness estimators by considering (a) the number of camera traps used in each survey; (b) the number of sampling stations (i.e., the number of different camera placements used during each survey); (c) the total sampling effort (the number of camera trap-days) at each locality; and (d) a null model. We determined the most parsimonious model based on Akaike’s information criterion, corrected for small sample size (AICc; Burnham et al. 2011). We selected the most plausible model using a Δ AICc < 2 and the higher relative contribution according to the Akaike Weight (ω). To assess the explanatory power of the model and corroborate that a model was better than the null model, we used the p-values of chi-squared tests considering the model’s deviance and residual degrees of freedom in the former, and the mathematical difference between deviances of both models and one degree of freedom for the latter. Finally, we calculated the variability explained by the best model as follows: 100 x (null deviance - residual deviance) / null deviance. We used the R package Glimulti (Calçagno and de Mazancourt 2010) for GLM calculations. We used the predict function in R software (R Core Team 2020) to calculate the minimum sampling effort necessary to reach the species richness of the long-term data at Tiquié (which was assumed to be a more complete survey of MLM by camera-trapping) according to the predicted species richness by the best estimator.

**RESULTS**

**Camera-trap sampling data**

Overall, 26 species of MLM were recorded in the 16 rapid assessments and the long-term survey at Tiquié, distributed in seven orders, 12 families, and 22 genera (Supplementary Material, Table S1). Five species were recorded most frequently and were present at most localities, being classified as core species: *Dasypus novemcinctus* Linnaeus, 1758 (23.1% of all independent records), *Cuniculus paca* (Linnaeus, 1766) (17.2%), *Tapirus terrestris* (Linnaeus, 1758) (15.2%), *Dasypus fuliginosus* Wagler, 1832 (14.2%), and *Pecari tajacu* (Linnaeus, 1758) (7.0%) (Figure 2). The remaining species were recorded in few localities and in low abundance and were classified as satellite species. The rarest satellite species, with only one record in one locality, were *Ateles cyncestus microtis* (Sclater, 1883) and *Hydrochoerus hydrochaeris* (Linnaeus, 1766) in lowland localities, and *Panthera onca* and *Nasua olivacea* (Gray, 1865) in Amazon foothill localities.

**Sampling completeness and species richness estimation**

The observed species richness per locality varied from five to 13 species. The highest richness was observed in Matavén (13 species), followed by Río Yarí and Lindosa (12 species each). Lowest richness was observed in Buenos Aires and Carrizal (five species each) (Table 2).

The species accumulation curves showed an increasing, non-asymptotical trend, indicating that a greater number of species was expected in all localities (Figure 3a). Sampling completeness varied among sites (ICE = 44 – 95%; Chao 2 = 50 – 100%; Jackknife 1 = 67 – 88%, Jackknife 2 = 50 – 91%) (Table 3). Estimated richness also varied among estimators (ICE = 5 – 22 species; Chao 2 = 5 – 20 species; Jackknife 1 = 6 – 17 species; Jackknife 2 = 7 – 19 species) (Table 2).

The long-term one-year survey at Tiquié recorded 21 species of MLM (Table 2; Supplementary Material, Table S1). Despite the longer sampling effort, all estimators for this dataset showed a similar, non-asymptotic trend in the accumulation curve, predicting that the actual species richness at Tiquié should be of 27 to 30 species (Figure 3b). This difference between estimated and observed richness may be owed to the presence of species with only one record in the survey. The comparison between the long-term and short-term survey data at Tiquié (Tables 1 and 2) showed that all estimators underestimated the species richness of the long-term survey (Figure 3c). The richness estimation at Tiquié with ICE, Jackknife 1, and Jackknife 2 was higher than with Chao 2 and, therefore, could better predict the species richness based on the short-term data (Figure 3c). The values for species richness using the four estimators varied among the rapid assessments. Chao 2 generally had...
the lowest values among the four estimators. Jackknife 1 values were intermediate and showed the least variation among localities, while ICE values fluctuated the most, and Jackknife 2 had the highest estimated richness values in most cases, showing a higher influence of singletons (Figure 3c). In addition to resulting in the more stable estimates, Jackknife 1 had the highest correlation between estimated and observed richness ($r = 0.96$), and the lowest correlation with singletons ($r = 0.82$) (Table 4), thus was the estimator less influenced by singletons. ICE had the lowest correlation between estimated

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**Table 2.** Recorded (N species) and estimated species richness according to four non-parametric estimators [ICE, Chao 2, Jackknife 1 (Jack 1), and Jackknife 2 (Jack 2)] for camera-trap rapid assessments at 16 localities in the Colombian Amazon. The percentage of completeness for all the estimators is also indicated.

| Location               | N species | ICE     | % ICE  | Chao 2 | % Chao 2 | Jack 1 | % Jack 1 | Jack 2 | % Jack 2 |
|------------------------|-----------|---------|--------|--------|----------|--------|----------|--------|----------|
| Andaki                 | 9         | 12.31   | 73.11  | 11.87  | 75.82    | 12.83  | 70.15    | 15.61  | 57.66    |
| Buenos Aires           | 5         | 5.27    | 94.88  | 5.00   | 100.00   | 5.96   | 83.89    | 6.88   | 72.67    |
| Calamar                | 9         | 12.94   | 69.55  | 9.98   | 90.18    | 11.95  | 75.31    | 12.95  | 69.59    |
| Carrizal               | 5         | 5.71    | 87.57  | 5.00   | 100.00   | 5.98   | 83.61    | 6.95   | 71.94    |
| Cerro Campana          | 6         | 6.49    | 92.45  | 6.00   | 100.00   | 6.97   | 86.08    | 7.00   | 85.71    |
| El Retorno             | 10        | 22.49   | 44.46  | 19.91  | 50.22    | 14.96  | 66.84    | 19.87  | 50.33    |
| Itilla                 | 7         | 7.42    | 94.34  | 7.00   | 100.00   | 7.98   | 87.72    | 8.00   | 87.50    |
| Lindosa                | 12        | 14.32   | 83.80  | 12.99  | 92.38    | 14.98  | 80.11    | 15.98  | 75.09    |
| Matavén                | 13        | 17.53   | 74.16  | 14.48  | 89.78    | 16.95  | 76.70    | 17.96  | 72.38    |
| Río Yari               | 12        | 14.70   | 81.63  | 14.94  | 80.32    | 15.92  | 75.38    | 18.83  | 63.73    |
| Sabanas del Yarí       | 7         | 12.46   | 56.18  | 9.98   | 70.14    | 9.98   | 70.14    | 12.93  | 54.14    |
| San José               | 11        | 12.37   | 88.92  | 11.25  | 97.78    | 12.98  | 84.75    | 12.03  | 91.44    |
| Sejal                  | 7         | 10.10   | 69.31  | 8.44   | 82.94    | 9.88   | 70.85    | 11.76  | 59.52    |
| Tiquié                 | 8         | 10.56   | 75.76  | 8.97   | 89.19    | 10.90  | 73.34    | 11.90  | 67.23    |
| Tunia                  | 9         | 15.31   | 58.78  | 10.95  | 82.19    | 12.90  | 69.77    | 14.86  | 60.56    |
| Yavaraté               | 6         | 9.65    | 62.18  | 8.84   | 67.87    | 8.84   | 67.87    | 11.53  | 52.04    |
| Tiquié (long term)     | 21        | 28.65   | 73.29  | 24.74  | 84.88    | 26.98  | 77.84    | 29.97  | 70.07    |
and observed richness ($r = 0.77$) and the highest correlation with singletons ($r = 0.89$). Chao 2 and Jackknife 2 have similar correlation values for observed and estimated richness ($r = 0.81$ and $0.83$, respectively), both lower than the values for Jackknife 1, and higher correlation with singletons than Jackknife 1 ($r = 0.86$ and $0.93$, respectively), showing a higher bias due to the presence of singletons (Table 3).

**Minimum sampling effort**

The GLM model that best explained the variation in species richness was based on total sampling effort (number of camera trap-days; $AICc = 83.82$, $ΔAICc$ to next model = 1.28, $w_AIC = 0.461$) (Table 4). The model explained $39\%$ of the data variance in the data, having strong explanatory power ($p$-value = $0.6098$) and differed significantly from the null model ($p$-value = $0.0247$). The model showed a positive effect (the number of recorded species increased with the number of camera trap-days). The second-best model had $ΔAICc < 2$ (Table 4), and was discarded as it included the number of stations and the number camera trap-days, but only the latter had a significant effect in the model.

According to the prediction function of the model and the species-richness estimates by the Jackknife 1 estimator, a minimum sampling effort of 350 camera trap-days would be necessary to record the number of species of the long-term survey at Tiquié (Figure 4).

**DISCUSSION**

Our results showed that the local species richness of medium and large terrestrial mammals in the northwestern Amazon in Colombia is still highly underestimated. We used an extensive dataset of local camera-trap rapid assessments which, individually, did not have enough sampling effort for an effective estimation of the species richness per locality. Yet, although completeness varied among localities, the assessments generally recorded the core species and some satellite species in each locality. Considering its climatic and ecosystemic heterogeneity, a higher diversity of MLM is expected for the Colombian Amazon beyond that recorded...
in our surveys and in some published inventories of MLM for the northwestern and southernmost portions of the region (e.g., Negret et al. 2015; Payán and Escudero-Páez 2015; Niño-Reyes and Velásquez-Valencia 2016; Lizcano et al. 2019; Atuesta-Dimian and Ganeden 2019; Atuesta-Dimian et al. 2020; Mena et al. 2020). Some of the latter studies were also based on a small sampling effort of less than 200 camera trap-days (e.g., Negret et al. 2015, Atuesta-Dimian and Ganeden 2019; Atuesta-Dimian et al. 2020).

Singletons influenced the estimators of species richness, including the long-term one-year dataset of Tiquié. The frequency occurrence of medium and large-sized mammals depends on the biological and behavioral characteristics of the species, which are related to demographic stochasticity, vagility, habitat preference, and the spatial and temporal variation in risk perception related to human activity (Henski 1982; Magurran and Henderson 2003). Apex predators, for example, have large home ranges, small population sizes, and their presence can be affected by human activity making them difficult to record with a small sampling effort (Maffei et al. 2011; Figueroa 2013). Therefore, rapid assessments might not be enough to detect these less abundant or rare species.

We recommend the use of the Jackknife 1 estimator in rapid assessments in the Colombian Amazon, based on its higher precision in the estimation of species richness of medium and large mammals in our samples, and the lower influence of singletons compared to the other tested estimators. Similarly, the Jackknife 1 has also been suggested as the best estimator in other rainforest studies of MLM (Tobler et al. 2008). However, taking sampling bias issues and the stochasticity of data acquisition into account, it should be advisable to always test survey data with multiple estimators. The non-parametric estimators used in this study had different performance according to the nature of the samples, but empirical species richness assessments seldom take this into account (González-Oreja et al. 2010). Therefore, biological richness studies should evaluate the behavior of estimators in order to choose the most appropriate depending on the taxonomic group and ecosystem studied. Our results also corroborate Colwell and Coddington (1994) in that rapid-assessment data should be calibrated with long-term data from comparable reference sites that use the same standardized sampling methods, if available. Multi-year long-term studies increase the accuracy of diversity estimates as they increase the probability of recording rare species.

The relative abundance of recorded species was heterogeneous among our sampling localities. *D. fuliginosa*, *C. paca*, *D. novemcinctus*, *P. tajacu*, and *T. terrestris* were locally abundant in most localities, showing their ample distribution in the wider region and their status as core mammal species in Colombian Amazon forests, as is the case in other parts of the Amazon (e.g., Tobler et al. 2008; Blake and Mosquera 2014; Scullion et al. 2021). Our results showed that the rapid assessments were suitable to document the presence of core species and give some insight into their local abundance, and also the presence of some satellite species. Due to their high abundance and biomass, in general, the most common species have an important role in the functionality and stability of ecosystems (Smith and Knapp 2003), and their abundance provides background information on the conservation status of the habitats in a locality. On the other hand, rare species, which are differentially underrepresented in rapid assessments, are most vulnerable to extinction (Purvis et al. 2000).

Colombian environmental policies, the limited funding of research institutions and environmental agencies, and the current need for rapid biodiversity assessments to take environmental decisions such as environmental licensing and the creation or enlargement of protected areas, require efficient and cost-effective studies that minimize the underestimation of ecological diversity estimates (e.g., Gómez-Sandoval et al. 2017). In most cases, short-term surveys are the only source of information that the environmental authorities have for decision making, therefore, they are crucial for the conservation and management of Colombian biodiversity, with the assessment of new conservation areas in the Orinoco Llanos (Mora-Fernández and Rodríguez-Posada 2017) and the extension of the Chiribiquete National Park in the Colombian Amazon (Atuesta-Dimian and Ganeden 2019) as recent examples. To strengthen the results of rapid assessments, we recommend a minimum sampling effort of 350 camera trap-days to reach a representative sample of the most common medium and large terrestrial mammals in Amazon-forest sites. We strongly suggest maximizing the sampling time because it increases the probability of capturing a higher number of rare species, allowing the calculation of detection probabilities and a more robust estimation of species richness (Kays et al. 2020).

It should be stressed that the results of short-term surveys do not measure the actual species richness of a locality. The
precise and accurate estimation of ecological parameters such as species richness and community structure, as well as population abundance and density, and species occupancy require long-term and large-scale sampling efforts (e.g., Tobler et al. 2008, 2013; Kays et al. 2020; Mena et al. 2020). A more accurate estimation of species richness and occupancy should be based on samplings longer than three weeks with more than 25 camera sites for common species, and more than 150 camera sites for rare species (Kays et al. 2020). Short-term surveys are necessary for environmental management in the Colombian Amazon and produce valuable information about biodiversity, but these data must be understood in the light of the representativeness of the sampling. More accurate estimates can be obtained using complementary methods to camera trapping, such as interviews with local inhabitants (Voss and Emmons 1996; López-Arévalo et al. 2021), surveys of animal tracks or signs (Fragoso et al. 2019), analysis of hunting records (Voss and Emmons 1996), and the prospection of remains of consumed animals that are usually available in indigenous and settler communities (Osorno et al. 2014). It is also important to stress that, although useful, rapid assessments are not enough to assess long-term effects of environmental transformation and tendencies of biodiversity loss. Therefore, besides determining minimum sampling standards that maximize the effectiveness of short-term assessments, it is crucial to also invest in standardized long-term surveys that allow evaluating processes at broader scales and making environmental decisions with solid scientific bases.

CONCLUSIONS

The local species richness of medium and large terrestrial mammals measured in 16 rapid assessments in the northwestern Amazon in Colombia was highly underestimated. Notwithstanding, rapid assessments provide richness information of good representativeness on core species and some satellite species in each locality. Our results indicate that the Jackknife-1 non-parametric estimator is the most accurate to estimate species richness in these kind of surveys in this region, due to its accurate estimation of richness and the low influence of singletons. We recommend a minimum sampling effort of 350 camera trap-days to achieve a representative estimate of species richness of medium and large terrestrial mammals in local surveys in the region, however precise ecological and populational assessments require larger sampling efforts.

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**SUPPLEMENTARY MATERIAL** (only available in the electronic version)

Morales-Martínez *et al*. Completeness of rapid assessments of medium and large mammal diversity in the northwestern Amazon in Colombia

**Table S1.** Relative abundance index for 26 medium and large terrestrial mammals with average body weight > 2 kg (excluding primarily arboreal species) recorded at 16 localities in the northwestern Amazon in Colombia through rapid camera-trapping assessments. The abundance index was calculated as the number of independent records/number of camera trap-days*100. N species = number of species per locality. Tiquié (long term) refers to a long-term dataset (a year-long sampling) (see Table 1 and Material and Methods).

| Species                      | Andakí | Buenos Aires | Calamar | Carrizal | Cerro Campana | Río Yari | El Retorno | Itilla | Lindosa | Matavén | San José | Sejal | Tiquié | Tunia | Sabanas del Yarí | Yavaraté | Tiquié (long term) |
|------------------------------|--------|--------------|---------|----------|---------------|----------|------------|--------|---------|---------|----------|-------|--------|-------|-----------------|----------|------------------|
| **Species**                  |        |              |         |          |               |          |            |        |         |         |          |       |        |       |                 |          |                  |
| Order Didelphimorphia        |        |              |         |          |               |          |            |        |         |         |          |       |        |       |                 |          |                  |
| Didelphis marsupialis        | 5.98   | 0.13         | 3.00    | 3.13     | 2.48          | 0.44     | 12.50      | 0.57   | 1.00    | 0.14    |          |       |        |       |                 |          |                  |
| **Species**                  |        |              |         |          |               |          |            |        |         |         |          |       |        |       |                 |          |                  |
| Order Cingulata              |        |              |         |          |               |          |            |        |         |         |          |       |        |       |                 |          |                  |
| Dasypus pastasae             | 1.79   |              | 8.44    | 0.83     | 11.67         |          |            |        |         |         |          |       |        |       |                 |          |                  |
| Dasypus novemcinctus         | 2.75   | 6.80         | 23.77   | 0.17     | 9.00          | 6.25     | 18.18      | 1.18   | 1.72    | 1.14    | 1.71     | 1.23  | 13.33  | 2.73  | 0.57            |          |                  |
| **Species**                  |        |              |         |          |               |          |            |        |         |         |          |       |        |       |                 |          |                  |
| Procyon maximus              | 0.85   |              | 0.44    |          |              |          |            |        |         |         |          |       |        |       |                 |          |                  |
| **Species**                  |        |              |         |          |               |          |            |        |         |         |          |       |        |       |                 |          |                  |
| Order Pilosa                 |        |              |         |          |               |          |            |        |         |         |          |       |        |       |                 |          |                  |
| Myrmecophaga tridactyla      | 0.85   |              | 1.00    | 0.65     | 1.11          |          |            |        |         |         |          |       |        |       |                 |          | 0.14             |
| Tamandua tetradactyla        | 0.65   | 4.96         | 1.11    | 1.14     | 1.23          | 1.23     | 1.00       | 0.47   |         |         |          |       |        |       |                 |          |                  |
| **Species**                  |        |              |         |          |               |          |            |        |         |         |          |       |        |       |                 |          |                  |
| Order Carnivora              |        |              |         |          |               |          |            |        |         |         |          |       |        |       |                 |          |                  |
| Atelocynus microtis          |        |              |         |          |               |          |            |        |         |         |          |       |        |       |                 |          | 1.23             |
| Cerdocyon thous              |        |              |         |          |               |          |            |        |         |         |          |       |        |       |                 |          | 0.88             |
| Eira barbara                 | 0.41   | 7.69         | 1.00    | 0.65     | 1.11          |          |            |        |         |         |          |       |        |       |                 |          | 0.95             |
| Leopardus pardalis           |        |              |         |          |               | 0.40     | 1.00       | 0.83   | 0.88    |          |          |       |        |       |                 |          | 0.43             |
| Leopardus wiedii             | 0.83   |              | 2.00    |          |              |          |            |        |         |         |          |       |        |       |                 |          | 1.67             |
| Nasua nasua                  | 0.41   |              | 1.65    | 0.56     |              |          |            |        |         |         |          |       |        |       |                 |          | 0.95             |
| Nasua olivacea               | 0.41   |              |         |          |              |          |            |        |         |         |          |       |        |       |                 |          |                  |
| Panthera onca                | 0.41   |              |         |          |              |          |            |        |         |         |          |       |        |       |                 |          | 0.47             |
| Puma concolor                |        |              |         |          |              |          |            |        |         |         |          |       |        |       |                 |          | 1.33             |
| **Species**                  |        |              |         |          |               |          |            |        |         |         |          |       |        |       |                 |          |                  |
| Order Perissodactyla          |        |              |         |          |               |          |            |        |         |         |          |       |        |       |                 |          |                  |
| Tapirus terrestris           | 5.83   | 2.50         | 8.00    | 18.75    | 2.48          | 0.44     | 5.68       | 9.14   | 9.88    | 143.33  | 1.00     | 2.84  |        |       |                 |          |                  |
| **Species**                  |        |              |         |          |               |          |            |        |         |         |          |       |        |       |                 |          |                  |
| Order Artiodactyla            |        |              |         |          |               |          |            |        |         |         |          |       |        |       |                 |          |                  |
| Mazama sp.                   |        |              |         |          |               | 1.25     | 1.00       | 1.56   | 0.44    | 1.23    |          |       |        |       |                 |          |                  |
| Mazama murelia               |        |              |         |          |               | 8.75     | 3.25       | 1.67   |          |         |          |       |        |       |                 |          | 0.14             |
| Mazama zamora                | 1.79   |              | 0.65    |          | 6.64          | 2.86     | 1.67       | 3.22   |          |         |          |       |        |       |                 |          |                  |
| Odocoileus cariacou          |        |              |         |          |               |          |            |        |         |         |          |       | 3.54   |       |                 |          |                  |
| Peccari tajacu               | 1.66   | 0.98         | 6.25    | 5.00     | 0.65          | 2.31     | 23.14      | 0.88   | 3.33    | 0.57    | 2.47     | 0.52  |        |       |                 |          |                  |
| Species                        | Andakí | Buenos Aires | Calamar | Carrizal | Cerro Campana | Rio Yari | El Retorno | Itilla | Lindosa | Matavén | San José | Sejal | Tiquié | Tunia | Sabanas del Yari | Yavaraté | Tiquié (long term) |
|-------------------------------|--------|--------------|---------|----------|---------------|----------|------------|---------|---------|---------|----------|-------|--------|-------|-------------------|----------|-------------------|
| Tayassu pecari                | 8.00   | 1.65         | 1.14    | 55.00    | 0.47          | 0.00     | 0.00       | 0.00   | 0.00    | 0.00    | 0.00     | 0.00  | 0.00   | 0.00  | 0.00               | 0.00     | 0.00              |
| Order Rodentia                |        |              |         |          |               |          |            |         |         |         |          |       |        |       |                   |          |                   |
| Cuniculus paca                | 1.24   | 6.80         | 11.97   | 0.21     | 13.75         | 7.00     | 5.84       | 18.75  | 22.31   | 7.52    | 3.89     | 2.27  | 1.14   | 2.71  | 5.00              | 7.27     | 147               |
| Dasyprocta fuliginosa         | 2.75   | 4.85         | 0.85    | 0.37     | 3.75          | 6.00     | 9.74       | 7.81   | 29.75   | 1.77    | 8.89     | 4.55  | 1.67   | 4.55  | 59.72             |          |                   |
| Hydrochoerus hydrochaeris    |        |              |         |          |               |          |            |         |         | 0.57    |          |       | 0.47   |       |                   |          |                   |
| Myoprocta acouchy             |        |              |         |          |               |          |            |         |         | 1.18    |          |       |        |       |                   |          |                   |
| Myoprocta pratti             | 0.83   |              |         |          |               |          |            |         |         | 1.14    |          | 0.47  |        |       |                   |          |                   |
| N species                     | 9      | 5            | 9       | 5         | 6             | 12       | 10         | 7      | 12      | 8       | 9        | 7     | 6      | 21    |                   |          |                   |