






ORIGINAL RESEARCH

Wildlife trail or systematic? Camera trap placement has little effect on estimates of mammal diversity in a tropical forest in Gabon

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Abstract

Camera traps (CTs) have been increasingly used for wildlife monitoring worldwide. In the tropics, most CT inventories target wildlife-friendly sites, and CTs are commonly placed towards wildlife trails. However, it has been argued that this placement strategy potentially provides biased results in comparison to more systematic or randomized approaches. Here, we investigated the impact of CT placement on the remotely sensed mammal diversity in a tropical forest in Gabon by comparing pairs of systematically placed and wildlife-trail-oriented CTs. Our survey protocol consisted of 15–17 sampling points arranged on a 2 km² grid and left for one month in the field. This protocol was replicated sequentially in four areas. Each sampling point comprised a CT pair: the ‘systematic CT’, installed at the theoretical point and systematically oriented towards the most uncluttered view; and the ‘trail CT’, placed within a 20-m radius and facing a wildlife trail. For the vast majority of species, the detection probabilities were comparable between placements. Species average capture rates were slightly higher for trail-based CTs, though this trend was not significant for any species. Therefore, the species richness and composition of the overall community, such as the spatial distribution patterns (from evenly spread to site-restricted) of individual species, were similarly depicted by both placements. Opting for a systematic orientation ensures that pathways used preferentially by some species—and avoided by others—will be sampled proportionally to their density in the forest undergrowth. However, trail-based placement is routinely used, already producing standardised data within large-scale monitoring programmes. Here, both placements provided a comparable picture of the mammal community, though it might not be necessarily true in depauperate areas. Both types of CT data can nevertheless be combined in multi-site analyses, since methods now allow accounting for differences in study design and detection bias in original CT data.

INTRODUCTION

Over the last decades, dramatic declines in wildlife populations have been reported worldwide (Ceballos et al., 2017; Collen et al., 2009; Craigie et al., 2010; Dirzo et al., 2014). These declines, and the overall degradation of natural ecosystems, are a direct consequence of growing

demographic pressure, unsustainable logging and hunting, urbanization and agricultural conversion (Edwards et al., 2019; Gillet et al., 2016; Hoffmann et al., 2010; Malhi et al., 2014; Sala et al., 2000).

In tropical Africa, massive losses of iconic megafauna, which includes flagship species such as elephants (*Loxodonta africana*) (Maisels et al., 2013) and the great apes

(*Gorilla spp.* and *Pan spp.*) (Strindberg et al., 2018) have been experienced. Species formerly considered less emblematic, such as pangolins (*Smutsia spp.* and *Phataginus spp.*), are also presently highly threatened (Heinrich et al., 2017; Mambeya et al., 2018). The spread of the illegal wildlife trade and modern hunting techniques up to the most isolated rural communities (Abernethy et al., 2013) has been promoted by the expansion of the road network for extractive activities, such as mining or logging (Kleinschroth et al., 2019). Production forests managed responsibly may, however, play an important buffer role, specifically in the periphery of protected areas, as long as integrated wildlife management is safeguarded and coupled with a strict control of forest access (Edwards et al., 2014; Lhoest et al., 2020). Continuous monitoring is essential in order to prioritise conservation actions both in well-protected areas and production forests, and user-friendly techniques and standardised methodologies are required to properly assess and monitor wildlife communities.

Camera traps (CTs) are used worldwide by scientists and private operators to study and monitor wildlife populations across a wide range of habitats and latitudes. Constant progress in technology, falling prices over time (Agha et al., 2018) and advances in data management software (Forrester et al., 2016; Scotson et al., 2017) have enabled the spread of this technique. In remote environments, such as tropical forests, the cost and time-efficiency of CTs, as well as their complementarity with other wildlife assessment methods, have been amply proven (Gogarten et al., 2020; Rovero & Marshall, 2009). CT inventories provide crucial information for wildlife managers on population state variables in a rapid and non-invasive manner. They allow the estimation of animal density for marked (Royle et al., 2009) and unmarked species (Howe et al., 2017; Nakashima et al., 2020; Rowcliffe et al., 2008), studying occurrence patterns through occupancy modelling (MacKenzie et al., 2017) and/or providing species capture rates, usually described with the relative abundance index (RAI) when standardised by the sampling effort.

To be comparable across space and time, CT studies should follow standardised, or at least comparable, approaches. In many surveys, the choice of CT location relies on subjective criteria based on accessibility or expectations of wildlife occurrence (Burton et al., 2015). More robust approaches relying on randomised or systematic sampling designs (e.g., regularly spaced grids with a predefined CT density) are also followed, sometimes applied across multiple sites, such as the TEAM monitoring network (Jansen et al., 2014). In most cases, the selection of the exact CT location is still based on the presence of wildlife trails or signs to select the “optimal”

location to capture the largest number of species, corresponding *de facto* to a non-random orientation (Cusack et al., 2015a; Kolowski & Forrester, 2017; TEAM Network, 2011). In contrast, a random orientation of CTs is needed for the density estimation of unmarked species using the random encounter model (REM) proposed by Rowcliffe et al. (2008) or the distance sampling approach described in Howe et al. (2017). This random orientation ensures that habitat features either bypassed or used preferentially by animals are representatively sampled in the forest undergrowth (Rowcliffe et al., 2013). Both REM and distance sampling methods have been successfully used for tropical species (Bessone et al., 2020; Cappelle et al., 2019; Cusack et al., 2015b; Gray, 2018).

Camera-related parameters such as trigger characteristics (Rovero et al., 2013) or inclination (Moore et al., 2020) are known to induce large fluctuations in detection, although there have been few studies on the impact of CT placement on detectability (Burton et al., 2015). Previous experiments have used an uncoupled design, which did not allow the dissociation of the effect of the placement from the effect of local habitat heterogeneity (Kays et al., 2009). In African savannahs, Cusack et al. (2015) used a spatially close paired design and found that inferences at the community scale were not biased, given a sufficient sampling effort. However, they recognised the need to replicate the approach in denser habitats, such as tropical forests. In the Neotropics, Blake and Mosquera (2014) and Di Bitetti et al. (2014) found contrasting impacts of pre-existing trails and roads (i.e., not natural wildlife trails) on the detected species diversity and community composition based on a relatively small sampling effort. More recently, Kolowski and Forrester (2017) showed that small-scale features in north American temperate forests, specifically fallen logs and wildlife trails, may significantly affect species detection. The question of whether CT surveys with different placement strategies provide comparable data at the species and community scales remains to be addressed in tropical forests.

Here, in a tropical forest in Gabon, where wildlife is diverse and abundant, we implemented a paired design composed of a systematically oriented camera and a trail-based camera, and developed a four-step approach for the analysis of paired CT data. Specifically, we tested whether the placement of the CT influences the overall species richness (step 1), and for individual species, the detectability and capture rate (RAI) (step 2). We expected a greater level of species richness and higher RAI for the trail placement by assuming the non-random movements of animals (species preferentially moving along wildlife trails) (Mann et al., 2015; Wearn et al., 2013). We also tested whether the CT placement influences the spatial distribution patterns (from evenly spread to site-

restricted) at the species and community scales (step 3), as well as the species composition of the detected mammal community (step 4). Overhunting has been demonstrated to result in depleted assemblages dominated by generalist taxa, with a size-selective defaunation gradient radiating from human settlements (Abernethy et al., 2013; Lhoest et al., 2020). Therefore, we also tested whether species body mass and conservation status, along with forest accessibility, drive these patterns.

METHODS

Study area

The study was conducted in eastern Gabon in the production forests granted to the Precious Woods Gabon - Compagnie Equatoriale des Bois, PWG-CEB, a logging company operating on approximately 600 000 ha with a 25-year cutting cycle. The company has established reduced-impact logging practises, harvesting on average 1.4 trees/ha ($\sim 10.4 \text{ m}^3/\text{ha}$ [Precious Woods - CEB, 2018]), and the Forest Stewardship Council and Pan-African Forest Certification labels, obtained in 2008 and 2017, respectively, require strict control of the impacts of logging on biodiversity. The concession encompasses old-growth evergreen forests in the northwest, near the Ivindo National Park (NP, Fig. 1A), as well as younger evergreen forests (dominated by *Aucoumea klaineana*) intertwined with included savannah patches in the southeastern part of the concession (Fig. 1B, brown patches). The total annual rainfall reaches 1710 mm, with a short dry season between June and August (Fick & Hijmans, 2017).

CT inventory

The CT inventory followed a grid design replicated sequentially in four areas (Fig. 1B) named according to the forest management unit to which they belong (BBD for Bambidie, OKJ for Okondja, and LLM for Lélama) and to the proximity of an old base camp (NDB for Ndambi). These inventories were implemented between September and December 2018, which corresponds to the long rainy season. Each grid was composed of 15–17 sampling points placed at a density of one per 2 km^2 (Fig. 1B, C) and left for one month in the field. To test the influence of the CT placement on the detected diversity, we set up a CT pair at each sampling point (Fig. 1D). The first camera (hereafter referred to as the ‘systematic camera’) was placed close to the theoretical position and systematically oriented towards the most naturally cleared area, which may or may not encompass a wildlife trail. The second camera (hereafter referred to as the ‘trail camera’) was installed within a 20 m radius

of the systematic camera to ensure a similar microhabitat, but was placed towards a wildlife trail or a crossing of several trails, following the TEAM recommendations (TEAM Network, 2011). The CTs (Bushnell Trophy Cam HD; Bushnell, Overland Park, KS, USA) were installed on trees at knee level (30–50 cm) and set up to record 5 s videos with a minimum trigger delay of 1 s between detection events. Surrounding grasses and lianas were cut within a 3 m radius of the camera to reduce false triggers while leaving the undergrowth mostly unchanged.

Species identification

Videos were processed into Camera Base version 1.7., an open access database (Tobler, 2015). Records of the same species were considered independent beyond a time interval of 30 min (Meek et al., 2014). Only mammals were considered for identification; mostly ground-dwelling species and a few semi-arboreal species were also included (Table 1). Species nomenclature followed the IUCN Red List of Threatened Species. Four species complexes were considered due to the difficulties in species identification on video: (1) the large-spotted genet complex comprises *Genetta servalina* and *Genetta maculata* (Hedwig et al., 2018); (2) the ‘mongoose’ species complex encompasses the long-nosed mongoose (*Herpestes naso*) and marsh mongoose (*Atilax paludinosus*) because they share similar habitats and show only slight anatomical differences (Wilson & Mittermeier, 2009); (3) the forest squirrel complex includes seven species from five different genera of the Sciuridae family, all showing small stature and similar coat patterns in the study area; (4) the last species complex corresponds to the ‘small pangolins’, because despite anatomical and colour differences, the long-tailed pangolin (*Phataginus tetradactyla*) and white-bellied pangolin (*Phataginus tricuspis*) were difficult to distinguish on night-time videos. Finally, for all detected species, the mean adult body mass was collected from Mittermeier et al. (2013) for primates, Wilson et al. (2016) for rodents, and Wilson and Mittermeier (Wilson et al., 2009; Wilson et al., 2011) for carnivores and hoofed mammals, and the conservation status was obtained from the IUCN Red List of Threatened Species.

Environmental and anthropogenic variables

Accessibility variables were derived for each CT by computing the distance to the nearest permanent logging road, national road, and village using ArcGIS software. In our study area, the entrances of logging roads are kept under surveillance, and access is restricted to company vehicles. We therefore considered this specific variable as a proxy for landscape fragmentation rather than human

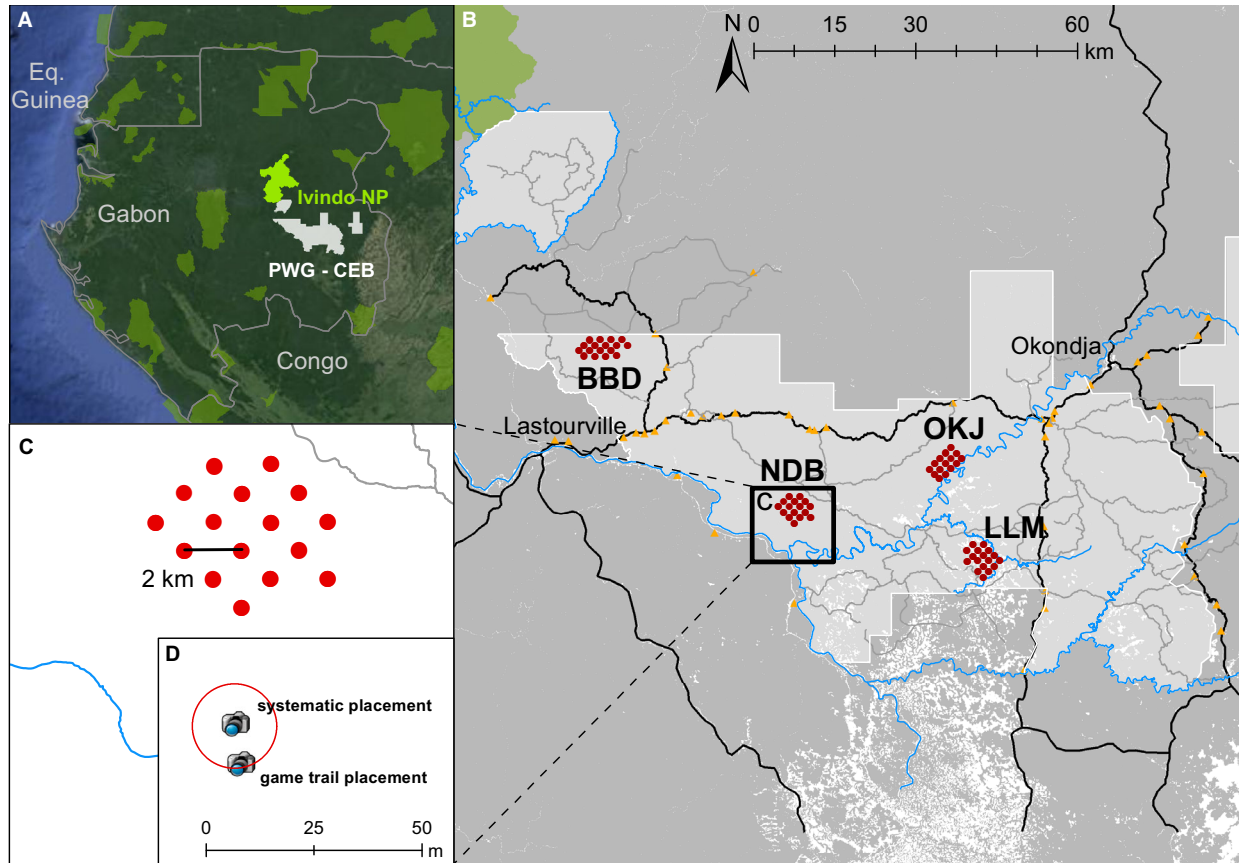


Figure 1. (A) Location of the PWG - CEB logging concession (in light grey) in Gabon and distribution of the protected area network (in green, the Ivindo NP is highlighted) on a Google Earth background map. (B) The location of the four CT grids, each composed of 15–17 sampling points (red dots), is shown on a background map of tree cover > 60% (Hansen et al., 2013). Major rivers (in blue), roads (national roads in black and main logging roads in grey), and villages (orange triangles) are also mapped. A zoom on the sampling design at the grid scale (density of installation = 1 camera site/2 km²) (C) and camera scale (pointing out the paired design) (D) is also provided.

disturbance. National roads, which cross almost the entire logging concession, and villages can be considered as proxies of landscape fragmentation and human pressure by acting as preferable access points for hunters.

Data analyses

To test the impact of the CT placement strategy on the remotely sensed mammal diversity, we developed a four-step approach targeting species richness (step 1), species detectability and capture rate (step 2), species and community–site association (step 3), and species composition (step 4). The environmental correlates were investigated in the last step (ordination, step 4).

First, we used sample-based rarefaction curves to test the effect of placement on species richness. The accumulation of species richness with cumulative sampling effort was performed at the grid scale using the *rarefy* function

of the *vegan* package (Oksanen et al., 2018). The Sørensen index of similarity was also computed using the *vegdist* function of *vegan* to evaluate species similarity between placements in each grid. Richness differences between CT pairs were also compared using a Wilcoxon signed-rank test.

Second, for each detected species (including the four species complexes), we generated the detection history (i.e., the sequence of detections and non-detections, MacKenzie et al., 2017) with the *camtrapR* package, considering 7-day sampling occasions (Niedballa et al., 2016). Then, we modelled the detection probability within a multi-method occupancy model (Nichols et al., 2008) using the *occMod* function of the *RPresence* package (MacKenzie & Hines, 2018). This modelling framework is particularly suited for paired design (Kolowski & Forrester, 2017). In addition to large-scale occupancy (ψ), which represents the probability that a focal species is

Table 1. List of detected species with the identifier (ID) used in the figures, IUCN status (listed as 'Least Concern' [LC], 'Near Threatened' [NT], 'Vulnerable' [VU], 'Endangered' [EN], or 'Critically Endangered' [CR]), and mean adult body mass following Mittermeier et al. (2013) for primates, Wilson et al. (2016) for rodents, and Wilson and Mittermeier (2009, 2011) for carnivores and hoofed mammals. The species average relative abundance index (RAI) and species site association (SSA) are given for each species and for each placement ('Syst' for systematic placement and 'Trail' for wildlife trail placement).

Order	Family	Species	ID	IUCN	Body mass (kg)	Population parameters in forest CTs			
						RAI		SSA	
						Syst	Trail	Syst	Trail
Artiodactyla									
	Bovidae	<i>Cephalophus callipygus</i>	1	LC	22.05	0.195	0.234	1.19	0.875
		<i>Cephalophus dorsalis</i>	2	NT	21.3	0.072	0.103	1.657	1.804
		<i>Cephalophus leucogaster</i>	3	NT	15.75	0.014	0.012	1.846	2.336
		<i>Cephalophus nigrifrons</i>	4	LC	14.5	0.001	0.001	/	/
		<i>Cephalophus ogilbyi</i>	5	LC	20	0.01	0.02	1.929	2.397
		<i>Cephalophus silvicultor</i>	6	NT	62.5	0.039	0.057	2.037	1.252
		<i>Neotragus batesi</i>	7	LC	2.5	0.001	/	/	/
		<i>Philantomba monticola</i>	8	LC	5	0.086	0.14	1.191	1.124
		<i>Syncerus caffer</i> ¹	9	NT	292.5	/	/	/	/
		<i>Tragelaphus scriptus</i> ¹	10	LC	52	/	/	/	/
	Suidae	<i>Potamochoerus porcus</i>	11	LC	80	0.032	0.035	1.917	1.623
	Tragulidae	<i>Hyemoschus aquaticus</i>	12	LC	11.5	0.024	0.018	2.858	2.976
Carnivora									
	Felidae	<i>Panthera pardus</i>	13	VU	46	/	0.002	/	/
		<i>Caracal aurata</i>	14	VU	11	0.003	0.006	3.892	3.48
	Herpestidae	<i>Bdeogale nigripes</i>	15	LC	3.4	0.005	0.004	4.625	3.306
		Mongoose	16	LC	3.2	0.007	0.007	2.964	2.488
	Nandiniidae	<i>Nandinia binotata</i> ²	17	LC	2.15	/	0.001	/	/
	Viverridae	<i>Civettictis civetta</i>	18	LC	13.5	0.002	0.001	/	/
		Large-spotted genet ²	19	LC	2.25	0.002	0.007	3.698	3.245
Pholidota									
	Manidae	<i>Smutsia gigantea</i>	20	EN	30	0.004	0.005	3.424	3.024
		Small pangolins ²	21	EN	2.55	0.002	0.002	/	/
Primates									
	Hominidae	<i>Gorilla gorilla</i> ²	22	CR	124	0.008	0.008	1.851	2.925
		<i>Pan troglodytes</i> ²	23	EN	45	0.025	0.026	1.788	1.547
Proboscidea									
	Elephantidae	<i>Loxodonta africana</i>	24	VU	4350	0.004	0.01	2.805	3.151
Rodentia									
	Hystricidae	<i>Atherurus africanus</i>	25	LC	2.9	0.059	0.08	1.389	1.863
	Nesomyidae	<i>Cricetomys emini</i>	26	LC	0.9	0.02	0.021	2.188	2.09
	Sciuridae	<i>Forest squirrels</i> ²	27	LC	0.65	0.019	0.019	2.328	2.113
	Thryonomyidae	<i>Thryonomys swinderianus</i>	28	LC	4.2	/	0.001	/	/
Tubulidentata									
	Orycteropodidae	<i>Orycteropus afer</i>	29	LC	52.5	/	0.001	/	/

¹Indicates savannah species

²Indicates semi-arboreal species

³Additional species observed in the study area through CTs (May 2019) or field observations: *Tragelaphus spekii*, *Mellivora capensis*, *Poiana richardsonii*, *Cercocebus agilis*, *Mandrillus sphinx*

present in the broad sampling area surrounding the CT pair (in our case, a circle of 0.707 km radius), the multi-method occupancy framework modelled an additional local occupancy parameter (θ) corresponding to the direct surroundings of the CT pair (Kolowski & Forrester, 2017; Nichols et al., 2008). To specifically investigate the impact

of CT placement on the detection probability, we selected the most likely multi-method occupancy model for each species using Akaike's Information Criterion corrected for small sample size (AIC_c; Hurvich & Tsai, 1995); however, we restricted this analysis to the 13 species presenting at least 10 independent detection events for each placement

(Ahumada et al., 2013). Specifically, we compared the general model with ψ , θ and p held constant to the model, considering the detection probability as placement-dependent. We additionally tested if the detection probability was different between grids and between placements and grids. Then, for each individual species and for each placement, we computed the RAI, which corresponds to the mean number of independent events per trap day and camera (Rovero & Marshall, 2009). We tested the influence of placement on the average RAI using Wilcoxon signed-rank test, and P -values were adjusted with the Benjamini–Hochberg correction, and we examined the systematic deviation (bias) using Bland–Altman concordance analysis. To integrate the heterogeneity of species RAI across CTs, we used a bootstrap approach. In each run ($n = 1000$), we sampled with replacement 43 CT pairs. We computed the species average RAI in each placement, and tested the correlation between placements using the Pearson coefficient. Finally, we computed the mean and quantiles of all 1000 correlations.

Third, we analysed site association (hereafter SSA) for species with at least three detections in each placement ($n = 19$) following a habitat specialization approach initially developed by Julliard et al. (2006). SSA corresponded to the coefficient of variation (standard deviation/mean) of species RAI across all CTs. Species spread evenly across the study area present a low SSA, whereas site-restricted species, detected only by a few CTs, showed high SSA. We tested the influence of species body mass and IUCN status on SSA using Tukey's HSD test within placements and Wilcoxon's signed-rank test between placements. A community–site association (CSA) index was then computed for each CT, which corresponded to the average site association of species found in the detected community. The CSA index revealed, therefore, the prevalence of site-restricted or evenly spread species. For both SSA and CSA, we tested the correlation between placements (Pearson's coefficient) and examined the systematic deviation (Bland–Altman analysis).

Finally, considering all CT data, we applied a non-metric multidimensional scaling using the *metaMDS* function in *vegan* (Oksanen et al., 2018) to examine the difference between placements in species composition. The dissimilarity matrix (Bray–Curtis index) was computed using the species RAI. Ecological dissimilarities among CTs within and between placements were analysed with respect to geographical distances between CTs. Environmental correlates, species richness and CSA were plotted as supplementary variables on the ordination.

All analyses were performed in R version R 3.6.1 (R Core Team, 2017) using the package *ggplot2* for plots (Wickham, 2016).

RESULTS

Inventory data

Preliminary analyses of the data showed that 111 (85%) of the 130 cameras deployed worked perfectly, that is operating more than 20 consecutive days and without the accumulation of moisture on the lens. Among those, 98 CTs (88%) were located in moist forests and 13 in included savannahs (Fig. 1B). A total of 3159 camera days were accumulated over the four consecutive inventories, allowing the detection of 25 terrestrial mammal species and four species complexes (Table 1), with a mean of 6 [1–14] species detected per CT. The detected species included taxa with strong conservation concerns, such as the critically endangered western lowland gorilla (*Gorilla gorilla gorilla*) or the giant pangolin (*Smutsia gigantea*). Some species, such as the central bushbuck (*Tragelaphus scriptus*) and African forest buffalo (*Syncerus caffer nanus*), were only detected in savannahs.

To test the impact of CT placement on species diversity and community composition, we only kept data from CT pairs that worked successfully and simultaneously. The CTs located in the included savannahs were also removed due to contrasting composition and too few replicates. The total sampling effort for all subsequent analyses was therefore 43 CT pairs in moist forest, totalling between 206 and 438 camera days for each placement (Fig. 2).

Impact of placement on species richness

Species richness was barely influenced by the CT placement, as shown by the large overlap between rarefaction curves, except for NDB (Fig. 2). The discrepancy in this specific area corresponded to scarcely detected species (with only three detections at most). Between 16 and 23 species were detected in each area and placement, with a strong similarity in the detected species (Sørensen index: 0.63–0.87). Similar richness was also reached between pairs according to the Wilcoxon signed-rank test ($p = 0.291$). Considering all data, four species were only detected by trail CTs; these were mostly elusive species, such as the leopard (*Panthera pardus*), with very few detection events (Table 1, species #13).

Impact of placement on species detection and capture rates

The CT placement did not impact the detection probabilities (p) for most species (Table 2a). Only *Cephalophus silvicultor* had a significantly greater detectability with trail CTs within each grid or over the whole study area (Table 2b). Variation in p between grids was supported

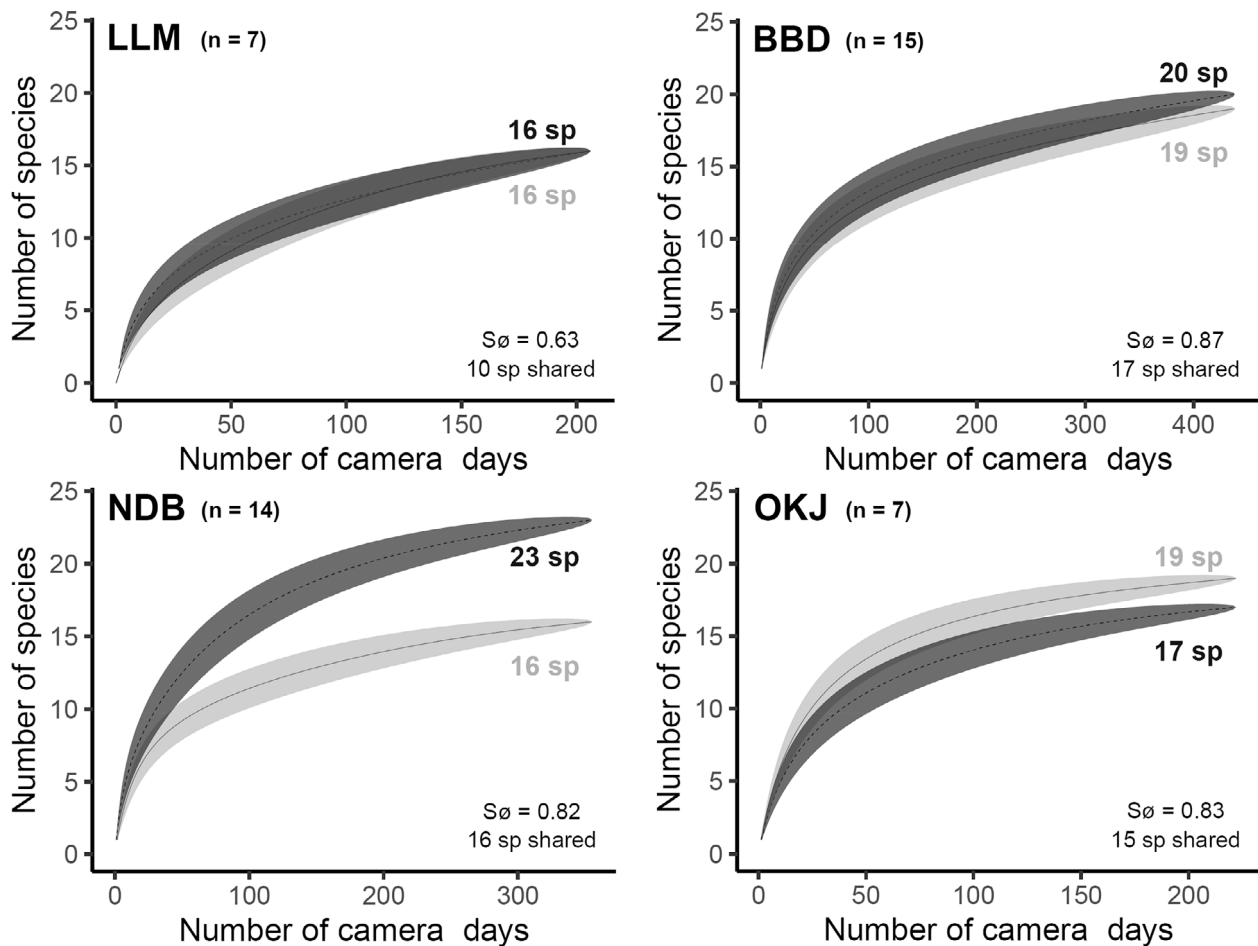


Figure 2. Rarefaction curves showing the accumulation of the number of mammal species detected in the four different areas as a function of the number of camera days. Grey and black lines correspond to systematic and trail CTs, respectively. Shaded polygons correspond to the standard deviation around the mean rarefied richness. The number of pairs in each area is given in parentheses. The Sørensen similarity index ($S\phi$) and number of shared species between placements are given at the bottom of each panel.

for seven species, and considered significant ($\Delta AICc > 2$, Burnham & Anderson, 2004) for five of them compared to the reference occupancy model ($\psi(\cdot)\theta(\cdot)p(\cdot)$) (Table 2a).

Using species average RAI rather than detection probabilities, the correlation between placements was even stronger ($r_{btp} = 0.97$), and most species presented slightly higher average RAIs (below the 1:1 line) for the trail CTs than for the systematic ones (Fig. 3). This was even more valid for the most captured species, such as the Peters's duiker (*Cephalophus callipygus*, #1) and blue duiker (*Philantomba monticola*, #8). This trend was corroborated by the positive relation (estimated slope = 0.26, $p < 0.001$) revealed by Bland–Altman analysis. However, the Wilcoxon signed-rank tests showed significant deviation for only two species, *Cephalophus silvicultor* and *Philantomba monticola*, which were no longer considered significant after P -value adjustment (all P values > 0.505). The variation between grids was weak and concerned infrequent

species, mostly detected only once or twice by one or the other placement (Fig. S1).

Impact of placement on site association of species and communities

For most species, the SSA index was significantly correlated between placements, revealing similar distribution patterns ($r = 0.83$, $p < 0.001$, Fig. 4A). The SSA varied from 0.87 to 4.62 between species evenly spread across the whole study area (e.g., the Peters's duiker, #1) and site-restricted ones (e.g., the black-legged mongoose, *Bdeogale nigripes*, #15). Infrequent species such as the golden cat, *Caracal aurata* [#14], were identified for both placements as site-restricted, with a high SSA value. The SSA was not found to be correlated with either species body mass (all P values > 0.816) or IUCN status (all P values > 0.242) within placements, and differences between

Table 2. (a) Multi-method occupancy model likelihood selection based on AIC_c for the 13 species with more than 10 detection events in both placements. Four occupancy models were compared: model (1), $\psi(\theta)\rho()$, model (2) considering p different between placements $\psi(\theta)\rho(\text{placement})$, model (3) considering p different between grids $\psi(\theta)\rho(\text{grid})$, and model (4) considering p different between placements and grids $\psi(\theta)\rho(\text{placement} + \text{grid})$. ΔAIC_c corresponds to the AIC_c difference between the given occupancy model and the reference occupancy model $\psi(\theta)\rho()$ and bold values represent a significant difference ($\Delta AIC_c > 2$). **(b)** Estimated p and associated 95% confidence interval of *Cephalophus silvicultor* for each grid and placement when considering the occupancy model $\psi(\theta)\rho(\text{placement} + \text{grid})$, and for each placement when considering the occupancy model $\psi(\theta)\rho(\text{placement})$.

(a)	Model	AIC_c	ΔAIC_c
Cephalophus callipygus	(1) $\psi(\theta)\rho()$	428.89	0
	(2) $\psi(\theta)\rho(\text{placement})$	429.37	-0.48
	(3) $\psi(\theta)\rho(\text{grid})$	434.9	-6.01
	(4) $\psi(\theta)\rho(\text{placement} + \text{grid})$	435.79	-6.9
Cephalophus dorsalis	(1) $\psi(\theta)\rho()$	370.56	0
	(2) $\psi(\theta)\rho(\text{placement})$	372.13	-1.57
	(3) $\psi(\theta)\rho(\text{grid})$	377.43	-6.87
	(4) $\psi(\theta)\rho(\text{placement} + \text{grid})$	379.43	-8.87
Cephalophus leucogaster ¹	(1) $\psi(\theta)\rho(\text{grid})$	188.95	7.12
	(2) $\psi(\theta)\rho(\text{placement} + \text{grid})$	191.67	2.28
	(3) $\psi(\theta)\rho()$	196.07	0
	(4) $\psi(\theta)\rho(\text{placement})$	198.35	-2.28
Cephalophus ogilbyi	(1) $\psi(\theta)\rho()$	169.48	0
	(2) $\psi(\theta)\rho(\text{placement})$	169.60	-0.12
	(3) $\psi(\theta)\rho(\text{grid})$	176.24	-6.76
	(4) $\psi(\theta)\rho(\text{placement} + \text{grid})$	176.84	-7.36
Cephalophus silvicultor ²	(1) $\psi(\theta)\rho(\text{placement} + \text{grid})$	329.86	4.14
	(2) $\psi(\theta)\rho(\text{placement})$	331.43	2.57
	(3) $\psi(\theta)\rho(\text{grid})$	332.28	1.72
	(4) $\psi(\theta)\rho()$	334	0
Philantomba monticola	(1) $\psi(\theta)\rho(\text{placement} + \text{grid})$	432.16	1.84
	(2) $\psi(\theta)\rho(\text{placement})$	432.54	1.46
	(3) $\psi(\theta)\rho(\text{grid})$	433.26	0.74
	(4) $\psi(\theta)\rho()$	434	0
Potamochoerus porcus ¹	(1) $\psi(\theta)\rho(\text{grid})$	248.53	4.82
	(2) $\psi(\theta)\rho(\text{placement} + \text{grid})$	250.73	2.62
	(3) $\psi(\theta)\rho()$	253.35	0
	(4) $\psi(\theta)\rho(\text{placement})$	255.05	-1.7
Hyemoschus aquaticus ¹	(1) $\psi(\theta)\rho(\text{placement} + \text{grid})$	92.01	7.16
	(2) $\psi(\theta)\rho(\text{grid})$	92.16	7.01
	(3) $\psi(\theta)\rho(\text{placement})$	98.67	0.5
	(4) $\psi(\theta)\rho()$	99.17	0
Gorilla gorilla	(1) $\psi(\theta)\rho()$	144.09	0
	(2) $\psi(\theta)\rho(\text{placement})$	146.46	-2.37
	(3) $\psi(\theta)\rho(\text{grid})$	150.05	-5.96
	(4) $\psi(\theta)\rho(\text{placement} + \text{grid})$	152.85	-8.76
Pan troglodytes ¹	(1) $\psi(\theta)\rho(\text{grid})$	230.3	14.53
	(2) $\psi(\theta)\rho(\text{placement} + \text{grid})$	233.16	11.67
	(3) $\psi(\theta)\rho()$	244.83	0
	(4) $\psi(\theta)\rho(\text{placement})$	247.26	-2.43
Atherurus africanus ¹	(1) $\psi(\theta)\rho(\text{grid})$	352.11	7.88
	(2) $\psi(\theta)\rho(\text{placement} + \text{grid})$	354.61	5.38
	(3) $\psi(\theta)\rho()$	359.99	0
	(4) $\psi(\theta)\rho(\text{placement})$	362.08	-2.09
Cricetomys emini	(1) $\psi(\theta)\rho(\text{grid})$	190.91	0.97
	(2) $\psi(\theta)\rho()$	191.88	0
	(3) $\psi(\theta)\rho(\text{placement} + \text{grid})$	193.71	-1.83

(Continued)

Table 2. Continued.

(a)				
	Model	AIC _c	ΔAIC _c	
Forest squirrels complex	(4) $\psi() \theta() p(\text{placement})$	194.26	-2.38	
	(1) $\psi() \theta() p(\text{grid})$	201.19	1.81	
	(2) $\psi() \theta() p()$	203	0	
	(3) $\psi() \theta() p(\text{placement} + \text{grid})$	204.02	-1.02	
	(4) $\psi() \theta() p(\text{placement})$	205.4	-2.4	
(b)				
	(1) $\psi() \theta() p(\text{placement} + \text{grid})$		(2) $\psi() \theta() p(\text{placement})$	
	p_{trail}	$p_{\text{systematic}}$	p_{trail}	$p_{\text{systematic}}$
BBD	0.46 [0.26–0.68]	0.27 [0.14–0.47]	0.64 [0.46–0.79]	0.45 [0.31–0.6]
LLM	0.53 [0.26–0.78]	0.33 [0.14–0.6]		
NDB	0.85 [0.64–0.95]	0.71 [0.47–0.87]		
OKJ	0.64 [0.37–0.84]	0.44 [0.22–0.69]		

¹Indicates species for which detection probabilities varied significantly between grids.

²Indicates the one particular species for which detection probabilities varied significantly with placement.

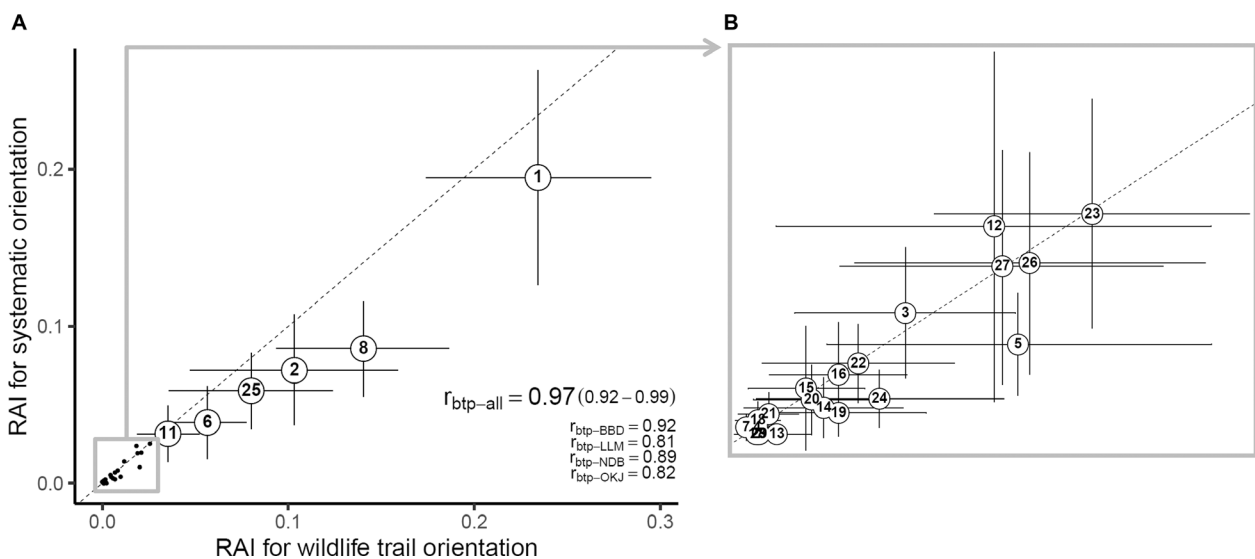


Figure 3. (A) Species average relative abundance index (RAI) in each placement strategy (systematic versus wildlife trail) considering all CT data and (B) zoom on the less detected species. One point represents one species, see Table 1 for species ID. Confidence intervals result from a bootstrap approach. In each run ($n = 10000$), we sampled with replacements 43 CTs and computed the species average RAI in each placement. Then, we computed the mean and quantiles of all 10000 means. The bootstrap Pearson correlation coefficient (rbtp) between species average RAI from both placements considering all CT data across the study area is given along with the 2.5% and 97.5% quantiles. The bootstrap Pearson correlation coefficient for each grid is also displayed.

placements were not significant (all P values >0.333). Community–site association assessed at the CT scale was well-correlated between placements ($r = 0.61$, $p < 0.001$, Fig. 4B), and the differences were mostly due to slight variation in species RAI within CT pairs and/or in SSA values between placements.

Impact of placement on community composition

Supporting earlier results, the CT placement had little impact on the overall species composition, as shown by a strong overlap in the ordination (Fig. 5). CTs presented a

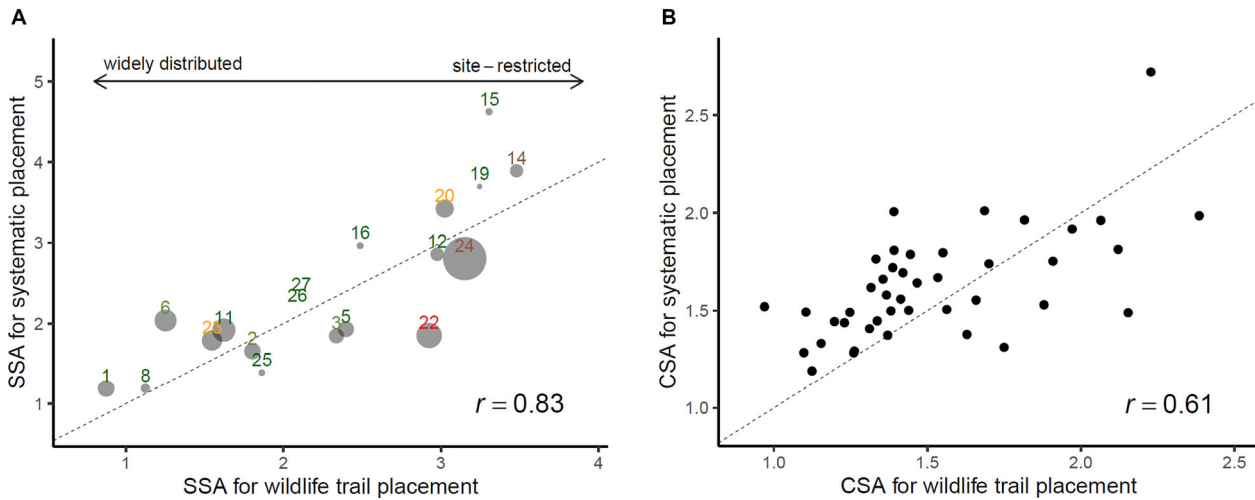


Figure 4. (A) Species site association (SSA) for each placement. One point represents one species, see Table 1 for species ID, and point size is proportional to the mean adult body mass. Species IDs are coloured according to the IUCN status (dark green for ‘Least Concern’ [LC], light green for ‘Near Threatened’ [NT], brown for ‘Vulnerable’ [VU], yellow for ‘Endangered’ [EN] and red for ‘Critically Endangered’ [CR]). (B) Community–site association (CSA) of each CT for each placement strategy. One point represents one sampling point (CT pair). The Pearson correlation coefficient (r) between both placements is given for both indices.

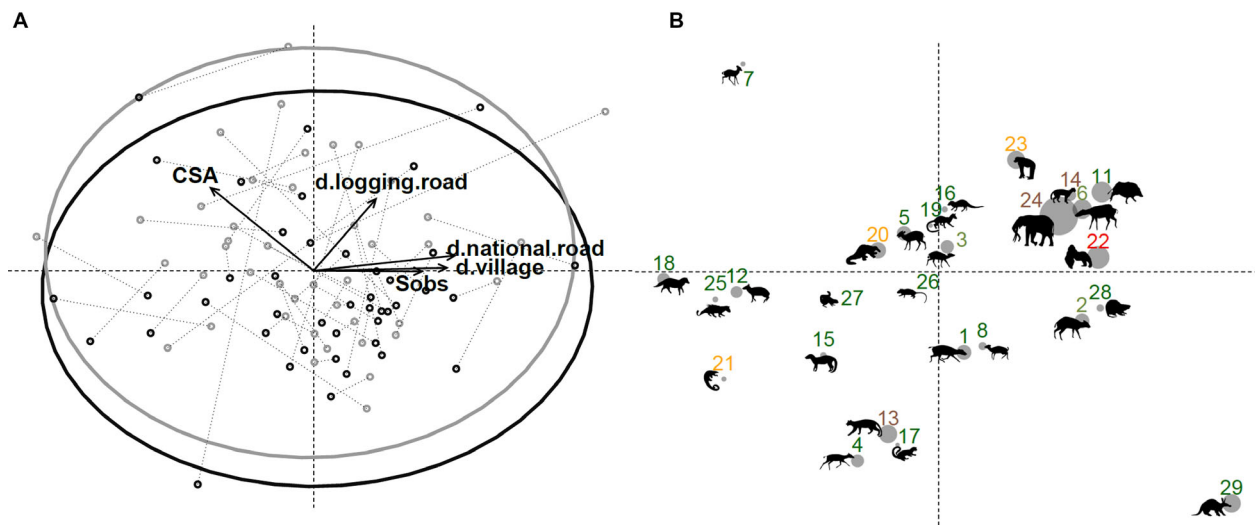


Figure 5. Non-metric multidimensional scaling analysis computed on the camera trap (CT) dissimilarity matrix, corresponding to the Bray–Curtis index computed using the species average relative abundance index (RAI). The locations of CTs (A) and species (B) are shown on the ordination axes. (A) Grey and black circles correspond to systematic and trail CTs, respectively. Paired CTs are joined with a dashed line. Arrows show the projection of supplementary variables: distance to the nearest permanent logging road (d.logging.road), distance to the nearest national road (d.national.road), distance to the nearest village (d.village), CSA, and species richness (Sobs). (B) Species averages on the ordination axes are shown with points proportional to the mean adult body mass (see Table 1 for species ID), and coloured according to the IUCN status (dark green for ‘Least Concern’ [LC], light green for ‘Near Threatened’ [NT], brown for ‘Vulnerable’ [VU], yellow for ‘Endangered’ [EN] and red for ‘Critically Endangered’ [CR]).

stronger similarity with their paired CT than with any other CTs (Fig. S2). Spatial variables related to human settlements and accessibility explained the first ordination axis (Fig. 5A) and the underlying gradient in species composition, corresponding to more vulnerable species

detected far from human settlements and roads. Indeed, the first ordination axis opposed communities with threatened or large-bodied species on the right, like the golden cat [#14], the gorilla [#22], and the forest elephant [#24], to communities with lower body mass species and

rodents such as the African brush-tailed porcupine (*Atherurus africanus*) [#25], Emin's pouched rat (*Cricetomys emini*) [#26], and forest squirrels [#27] (Fig. 5B).

DISCUSSION

CT technology has enabled a tremendous leap forward for monitoring medium- to large-bodied terrestrial mammals in remote areas as complex and diversified as tropical moist forests. Although species characteristics (Harmsen et al., 2010; Rowcliffe et al., 2011), abiotic factors (Noss et al., 2003) and camera-related parameters (McIntyre et al., 2020; Moore et al., 2020; Rovero et al., 2013) have been shown to influence the detection process, the impact of the placement strategy on the detected diversity has been little studied in tropical forests. Here, we demonstrated that the CT placement had little impact on species richness and composition and provided a similar picture of the particularly rich ground-dwelling mammal community in a tropical forest in Gabon. At the species level, detectability was similar for most species, but capture rates were found to be slightly, but not significantly, impacted by the CT placement, with higher species RAI when CTs were placed towards wildlife trails.

The total number of detected species was very close between placements, with a high proportion of shared species. The small remaining differences concerned elusive species occurring naturally at low densities (e.g., leopard), which is congruent with the results obtained by Cusack et al. (2015) in savannahs. In most surveyed areas, CTs placed on wildlife trails did not accumulate new species faster than those placed systematically, which is contrary with observations in savannahs (Cusack et al., 2015) and temperate forests (Kolowski & Forrester, 2017). Even though a proper comparison between production and protected forests was not implemented in this study, the studied forest holds a rich and well-preserved fauna with species richness levels similar to the updated species lists of the surrounding protected areas in Gabon, namely the Ivindo, Minkébé, and Mwagna NPs (Vandeweghe et al., 2016). This result confirms the previously highlighted potential conservation role of production forests (Putz et al., 2012).

Beyond species richness, wildlife managers are often looking for estimations of wildlife abundance, a key parameter in monitoring programmes. The non-random deployment of CTs in the field, which is particularly common across the tropics, may, however, provide a flawed picture of the community due to differential travelling habits between species (Mann et al., 2015). Large carnivores may prefer trails as travel routes and are therefore more often captured with trail-based CTs, even though

this is not always the case for their prey (Harmsen et al., 2010; Mann et al., 2015). Similar-sized species that share comparable ecological niches (e.g., wild Bornean felid species) may also display different space use patterns, resulting in contrasting detection frequencies between placement strategies (Wearn et al., 2013). In our study, detection probabilities based on presence data were not substantially influenced by placement, but trail-based cameras provided a slightly higher RAI for most species, though the difference was not significant. All trophic guilds followed this trend here, while in savannahs, Cusack et al. (2015) considered this deviation as only significant for carnivores. A significant shift in the rank species occupy in the detected community was also observed by Cusack et al. (2015) when comparing random and trail-based CTs. Here, the RAI shift only started from the eighth species, with the dominant species being similarly ranked. The RAI is an extensive, but controversial, method of valuing CT data (Burton et al., 2015). Apart from the true population density, a range of variables, such as animal-specific factors (body mass, behaviour, space use, etc.) and the characteristics of the detection area (e.g., vegetation density and the presence of trails) may induce fluctuations in capture rates (Broadley et al., 2019; Hofmeester et al., 2019). Together, these variables induced imperfect species detection, which is probably not uniform across populations (O'Brien, 2011). The RAI is therefore more comparable to a predictor of microhabitat use, reflecting both density and movement, rather than a suitable surrogate of local abundance (Broadley et al., 2019; Hofmeester et al., 2019). Finally, based on an important sampling effort (43 paired CTs), we also concluded that the overall detected mammal community was similar between placements in terms of species composition, which is congruent with the previous study of Blake and Mosquera (2014) in Ecuador.

The apparent weak effect of CT placement strategy on the detected species and communities reported here may arise from the distinct but non-exclusive explanations listed below. The first explanation is linked to the forest understory structure surrounding the CT, which may induce locally different travelling patterns between and within species by channelling animal movements through trails in a particularly dense environment (Harmsen et al., 2010). Vegetation, by restraining the transmission of infrared radiation towards the sensor, may also induce local variation in detectability (Hofmeester et al., 2017). Although we did not properly characterise the visibility within the CT detection area, the very short distance between paired CTs ensured a similar undergrowth, and vegetation density at the CT scale was therefore assumed to be comparable within pairs. The second explanation is linked to the abundant wildlife populations present in the

study area and the associated dense network of wildlife trails. In places where hunting pressure has already led to depauperate wildlife assemblages (Benítez-López et al., 2019; Ziegler et al., 2016), trails could be more scarcely and unevenly distributed, leading possibly to contrasting results. The third explanation is linked to the spatial use of species. Different species can display different micro-habitat preferences, and species detection might be influenced by the affinity of individual species for different types of trails (e.g. Harmsen et al., 2010; Wearn et al., 2013; Weckel et al., 2006). Trail size has been demonstrated to be positively correlated with capture rates for cats in Belize, while some of their potential prey showed the opposite trend (Harmsen et al., 2010). In temperate forests, Kolowski and Forrester (2017) also showed the substantial impact of trails, specifically larger and well-defined ones, on the detection of white-tailed deer. In savannahs, Cusack et al. (2015) only considered trails as continuous bare routes larger than 1 m, with recent signs of use. In this study, wildlife trails were narrower (<1 m), and like in Blake and Mosquera (2014), easily blended into the undergrowth background.

Beyond these factors, other confounding variables associated with the consensus required by multi-species monitoring, such as the trap density (grid size) or the sampling effort, might have impacted detectability (Hofmeester et al., 2019). The selected CT spacing may be optimal for certain target species but not for others (Foster & Harmsen, 2012). Here, we followed the grid size recommended by the TEAM Network, which represents a compromise for ground-dwelling vertebrates in the tropics. However, highly mobile species with large home ranges (e.g., forest elephants) and occurring sometimes at low densities (e.g., leopards) might be missed or underestimated with such a design. Home range size, which remains scarcely known for tropical species, has already been shown to induce variation in detection between species through simulations (Sollmann et al., 2013). A few more relevant animal characteristics that might bias detection probabilities were listed by Hofmeester et al. (2019): day movement rates, directionality and speed of movement, and resource availability. All are known to be related to two important life-history traits, animal diet and body mass (Carbone et al., 2005; Rowcliffe et al., 2016), which can easily be integrated into a modelling approach of CT data (Hofmeester et al., 2019). The semi-arboreal or fossorial behaviour of some species might also lead to disparities in the detection process according to the time these species spent on the ground (Hofmeester et al., 2019). Often marginalised in CT surveys, the limited availability of these species could be addressed by quantifying their activity levels and accounting for it in the computation process (Rowcliffe et al., 2014). Because of these specificities, adapted protocols might therefore be preferred for specific taxa, as already

implemented for wild cats (see Bahaa-el-din et al., 2016; Henschel et al., 2014) and pangolins (Willcox et al., 2019).

CONCLUSION

While multi-species monitoring is challenging, especially in tropical forests, camera trapping constitutes a non-invasive and efficient inventory method. Several factors influence the detection process, and systematic CTs undoubtedly provide a more robust sampling strategy when inferences at larger scales are of prime concern, especially since the travelling patterns of most tropical species remain unknown. However, a trail-based approach is still commonly used, and complete random placement is frequently discarded for fear of no/few detections. A major conclusion of this study is that species detection and capture rates are only barely influenced by the CT placement when the wildlife populations are abundant and the associated network of wildlife trails is dense. It might not be necessarily true in depauperate areas, and accounting for differences in study design and detection bias in CT data analysis might be required for multi-site comparisons.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

REFERENCES

- Abernethy, K.A., Coad, L., Taylor, G., Lee, M.E. & Maisels, F. (2013) Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **368**, 20120303.
- Agha, M., Batter, T., Bolas, E.C., Collins, A.C., Gomes da Rocha, D., Monteza-Moreno, C.M. et al. (2018) A review of wildlife camera trapping trends across Africa. *African Journal of Ecology*, **56**, 694–701.
- Ahumada, J.A., Hurtado, J. & Lizcano, D. (2013) Monitoring the status and trends of tropical forest terrestrial vertebrate communities from camera trap data: a tool for conservation. *PLoS One*, **8**, e73707.
- Bahaa-el-din, L., Sollmann, R., Hunter, L.T.B., Slotow, R., Macdonald, D.W. & Henschel, P. (2016) Effects of human land-use on Africa's only forest-dependent felid: The African golden cat *Caracal aurata*. *Biological Conservation*, **199**, 1–9.
- Benítez-López, A., Santini, L., Schipper, A.M., Busana, M. & Huijbregts, M.A. (2019) Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics. *PLoS Biology*, **17**, e3000247.
- Bessone, M., Kühl, H.S., Hohmann, G., Herbinger, I., N'Goran, K.P., Asanzi, P. et al. (2020) Drawn out of the shadows: Surveying secretive forest species with camera trap distance sampling. *Journal of Applied Ecology*, **57**, 963–974.
- Blake, J.G. & Mosquera, D. (2014) Camera trapping on and off trails in lowland forest of eastern Ecuador: does location matter? *Mastozoology Neotropical*, **21**, 17–26.
- Broadley, K., Burton, A.C., Avgar, T. & Boutin, S. (2019) Density-dependent space use affects interpretation of camera trap detection rates. *Ecology and Evolution*, **9**, 14031–14041.
- Burnham, K.P. & Anderson, D.R. (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research*, **33**, 261–304.
- Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T. et al. (2015) Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, **3**, 675–685.
- Cappelle, N., Després-Einspenner, M.-L., Howe, E.J., Boesch, C. & Kühl, H.S. (2019) Validating camera trap distance sampling for chimpanzees. *American Journal of Primatology*, **81**, e22962.
- Carbone, C., Cowlshaw, G., Isaac, N.J. & Rowcliffe, J.M. (2005) How far do animals go? Determinants of day range in mammals. *American Naturalist*, **165**, 290–297.
- Ceballos, G., Ehrlich, P.R. & Dirzo, R. (2017) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, **114**, E6089–E6096.
- Collen, B., Loh, J., Whitmee, S., McRAE, L., Amin, R. & Baillie, J.E.M. (2009) Monitoring change in vertebrate abundance: the Living planet index. *Conservation Biology*, **23**, 317–327.
- Craigie, I.D., Baillie, J.E.M., Balmford, A., Carbone, C., Collen, B., Green, R.E. et al. (2010) Large mammal population declines in Africa's protected areas. *Biological Conservation*, **143**, 2221–2228.
- Cusack, J.J., Dickman, A.J., Rowcliffe, J.M., Carbone, C., Macdonald, D.W. & Coulson, T. (2015a) Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. *PLoS One*, **10**, e0126373.
- Cusack, J.J., Swanson, A., Coulson, T., Packer, C., Carbone, C., Dickman, A.J. et al. (2015b) Applying a random encounter model to estimate lion density from camera traps in Serengeti National Park, Tanzania. *The Journal of Wildlife Management*, **79**, 1014–1021.
- Di Bitetti, M.S., Paviolo, A. & De Angelo, C. (2014) Camera trap photographic rates on roads vs. off roads: location does matter. *Mastozoology Neotropical*, **21**, 37–46.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014) Defaunation in the Anthropocene. *Science*, **345**, 401–406.
- Edwards, D.P., Socolar, J.B., Mills, S.C., Burivalova, Z., Koh, L.P. & Wilcove, D.S. (2019) Conservation of tropical forests in the anthropocene. *Current Biology*, **29**, R1008–R1020.
- Edwards, D.P., Tobias, J.A., Sheil, D., Meijaard, E. & Laurance, W.F. (2014) Maintaining ecosystem function and services in logged tropical forests. *Trends in Ecology & Evolution*, **29**, 511–520.
- Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, **37**, 4302–4315.
- Forrester, T., O'Brien, T., Fegraus, E., Jansen, P.A., Palmer, J., Kays, R. et al. (2016) An open standard for camera trap data. *Biodiversity Data Journal*, **4**, e10197.
- Foster, R.J. & Harmsen, B.J. (2012) A critique of density estimation from camera-trap data. *The Journal of Wildlife Management*, **76**, 224–236.
- Gillet, P., Vermeulen, C., Feintrenie, L., Dessard, H. & Garcia, C. (2016) Quelles sont les causes de la déforestation dans le bassin du Congo ? Synthèse bibliographique et études de cas. *Biotechnologie, Agronomie, Société et Environnement*, **20**, 183–194.
- Gogarten, J.F., Hoffmann, C., Arandjelovic, M., Sachse, A., Merkel, K., Dieguez, P. et al. (2020) Fly-derived DNA and camera traps are complementary tools for assessing mammalian biodiversity. *Environmental DNA*, **2**, 63–76.
- Gray, T.N.E. (2018) Monitoring tropical forest ungulates using camera-trap data. *Journal of Zoology*, **305**, 173–179.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., et al. (2013). High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853.

- Harmsen, B.J., Foster, R.J., Silver, S., Ostro, L. & Doncaster, C.P. (2010) Differential use of trails by forest mammals and the implications for camera-trap studies: a case study from Belize. *Biotropica*, **42**, 126–133.
- Hedwig, D., Kienast, I., Bonnet, M., Curran, B.K., Courage, A., Boesch, C. et al. (2018) A camera trap assessment of the forest mammal community within the transitional savannah-forest mosaic of the Batéké Plateau National Park, Gabon. *African Journal of Ecology*, **56**, 777–790.
- Heinrich, S., Wittman, T.A., Ross, J.V., Shepherd, C.R., Challender, D.W.S. & Cassey, P. (2017). The global trafficking of pangolins : A comprehensive summary of seizures and trafficking routes from 2010–2015.
- Henschel, P., Malanda, G.-A. & Hunter, L. (2014) The status of savanna carnivores in the Odzala-Kokoua National Park, northern Republic of Congo. *Journal of Mammalogy*, **95**, 882–892.
- Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T.M., Butchart, S.H.M. et al. (2010) The impact of conservation on the status of the World's vertebrates. *Science*, **330**, 1503–1509.
- Hofmeester, T.R., Cromsigt, J.P., Odden, J., Andrén, H., Kindberg, J. & Linnell, J.D. (2019) Framing pictures: A conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. *Ecology and Evolution*, **9**, 2320–2336.
- Hofmeester, T.R., Rowcliffe, J.M. & Jansen, P.A. (2017) A simple method for estimating the effective detection distance of camera traps. *Remote Sensing in Ecology and Conservation*, **3**, 81–89.
- Howe, E.J., Buckland, S.T., Després-Einspenner, M.-L. & Kühl, H.S. (2017) Distance sampling with camera traps. *Methods in Ecology and Evolution*, **8**, 1558–1565.
- Hurvich, C.M. & Tsai, C.-L. (1995) Model selection for extended quasi-likelihood models in small samples. *Biometrics*, **53**, 1077–1084.
- Jansen, P.A., Ahumada, J., Fegraus, E. & O'Brien, T. (2014) TEAM: a standardised camera trap survey to monitor terrestrial vertebrate communities in tropical forests. *Camera Trapping: Wildlife Management and Research*. Collingwood, Australia: CSIRO Publishing, pp. 263–270.
- Julliard, R., Clavel, J., Devictor, V., Jiguet, F. & Couvet, D. (2006) Spatial segregation of specialists and generalists in bird communities. *Ecology Letters*, **9**, 1237–1244.
- Kays, R., Kranstauber, B., Jansen, P., Carbone, C., Rowcliffe, M., Fountain, T. et al. (2009) *IEEE 34th Conference on Local Computer Networks (LCN 2009)*. Zurich, Switzerland: IEEE, pp. 811–818.
- Kleinschroth, F., Laporte, N., Laurance, W.F., Goetz, S.J. & Ghazoul, J. (2019) Road expansion and persistence in forests of the Congo Basin. *Nature Sustainability*, **2**, 628–634.
- Kolowski, J.M. & Forrester, T.D. (2017) Camera trap placement and the potential for bias due to trails and other features. *PLoS One*, **12**, e0186679.
- Lhoest, S., Fonteyn, D., Daïnou, K., Delbeke, L., Doucet, J.-L., Dufrière, M. et al. (2020) Conservation value of tropical forests: Distance to human settlements matters more than management in Central Africa. *Biological Conservation*, **241**, 108351.
- MacKenzie, D. & Hines, J. (2018). RPresence: R Interface for Program PRESENCE.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L. & Hines, J.E. (2017) *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*, 2nd. ed. edition. London, UK: Academic Press.
- Maisels, F., Strindberg, S., Blake, S., Wittemyer, G., Hart, J., Williamson, E.A. et al. (2013) Devastating decline of forest elephants in Central Africa. *PLoS One*, **8**, e59469.
- Malhi, Y., Gardner, T.A., Goldsmith, G.R., Silman, M.R. & Zelazowski, P. (2014) Tropical forests in the Anthropocene. *Annual Review of Environment and Resources*, **39**, 125–159.
- Mambeya, M.M., Baker, F., Momboua, B.R., Koumba Pambo, A.F., Hega, M., Okouyi Okouyi, V.J. et al. (2018) The emergence of a commercial trade in pangolins from Gabon. *African Journal of Ecology*, **56**, 601–609.
- Mann, G.K.H., O'Riain, M.J. & Parker, D.M. (2015) The road less travelled: assessing variation in mammal detection probabilities with camera traps in a semi-arid biodiversity hotspot. *Biodiversity and Conservation*, **24**, 531–545.
- McIntyre, T., Majelantle, T.L., Slip, D.J. & Harcourt, R.G. (2020) Quantifying imperfect camera-trap detection probabilities: implications for density modelling. *Wildlife Research*, **47**, 177–185.
- Meek, P.D., Ballard, G., Claridge, A., Kays, R., Moseby, K., O'Brien, T., et al. (2014) Recommended guiding principles for reporting on camera trapping research. *Biodiversity and Conservation*, **23**, 2321–2343.
- Mittermeier, R.A., Rylands, A.B. & Wilson, D.E. (Eds.) (2013). *Handbook of the Mammals of the World*. Vol. 3. Primates, Lynx Edicions. ed. Barcelona, Spain.
- Moore, H.A., Valentine, L.E., Dunlop, J.A. & Nimmo, D.G. (2020) *The effect of camera orientation on the detectability of wildlife: a case study from north-western Australia*. Conserv: Remote Sens. Ecol.
- Nakashima, Y., Hongo, S. & Akomo-Okoue, E.F. (2020) Landscape-scale estimation of forest ungulate density and biomass using camera traps: Applying the REST model. *Biological Conservation*, **241**, 108381.
- Nichols, J.D., Bailey, L.L., O'Connell, A.F. Jr, Talancy, N.W., Campbell Grant, E.H., Gilbert, A.T. et al. (2008) Multi-scale occupancy estimation and modelling using multiple detection methods. *Journal of Applied Ecology*, **45**, 1321–1329.
- Niedballa, J., Sollmann, R., Courtiol, A. & Wilting, A. (2016) camtrapR: an R package for efficient camera trap data management. *Methods in Ecology and Evolution*, **7**, 1457–1462.
- Noss, A.J., Cuéllar, R.L., Barrientos, J., Maffei, L., Cuéllar, E., Arispe, R. et al. (2003) A camera trapping and radio

- telemetry study of lowland tapir (*Tapirus terrestris*) in Bolivian dry forests. *Tapirus Conservation*, **12**, 24–32.
- O'Brien, T.G. (2011) Abundance, density and relative abundance: a conceptual framework. *Camera Traps in Animal Ecology*. Springer, 71–96.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P. & McGlinn, D. et al. 2019. Vegan: Community ecology package. 2018.
- Precious Woods - CEB, (2018) Rapport annuel 2018. Suivi-Évaluation des indicateurs de performance environnementale CFAD Precious Woods -CEB.
- Putz, F.E., Zuidema, P.A., Synnott, T., Peña-Claros, M., Pinard, M.A., Sheil, D. et al. (2012) Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conservation Letters*, **5**, 296–303.
- R Core Team, 2017. R: A language and environment for statistical computing.
- Rovero, F. & Marshall, A.R. (2009) Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology*, **46**, 1011–1017.
- Rovero, F., Zimmermann, F., Berzi, D. & Meek, P. (2013) “Which camera trap type and how many do I need?” A review of camera features and study designs for a range of wildlife research applications. *Hystrix*, **24**, 148–156.
- Rowcliffe, J.M., Carbone, C., Jansen, P.A., Kays, R. & Kranstauber, B. (2011) Quantifying the sensitivity of camera traps: an adapted distance sampling approach. *Methods in Ecology and Evolution*, **2**, 464–476.
- Rowcliffe, J.M., Field, J., Turvey, S.T. & Carbone, C. (2008) Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, **45**, 1228–1236.
- Rowcliffe, J.M., Jansen, P.A., Kays, R., Kranstauber, B. & Carbone, C. (2016) Wildlife speed cameras: measuring animal travel speed and day range using camera traps. *Remote Sensing in Ecology and Conservation*, **2**, 84–94.
- Rowcliffe, J.M., Kays, R., Carbone, C. & Jansen, P.A. (2013) Clarifying assumptions behind the estimation of animal density from camera trap rates. *The Journal of Wildlife Management*, **77**, 876–876.
- Rowcliffe, J.M., Kays, R., Kranstauber, B., Carbone, C. & Jansen, P.A. (2014) Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution*, **5**, 1170–1179.
- Royle, J.A., Nichols, J.D., Karanth, K.U. & Gopalaswamy, A.M. (2009) A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology*, **46**, 118–127.
- Sala, O.E., Chapin, F.S. III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R. et al. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- Scotson, L., Johnston, L.R., Iannarilli, F., Wearn, O.R., Mohd-Azlan, J., Wong, W.M. et al. (2017) Best practices and software for the management and sharing of camera trap data for small and large scales studies. *Remote Sensing in Ecology and Conservation*, **3**, 158–172.
- Sollmann, R., Mohamed, A., Samejima, H. & Wilting, A. (2013) Risky business or simple solution—Relative abundance indices from camera-trapping. *Biological Conservation*, **159**, 405–412.
- Strindberg, S., Maisels, F., Williamson, E.A., Blake, S., Stokes, E.J., Aba'a, R. et al. (2018). Guns, germs, and trees determine density and distribution of gorillas and chimpanzees in Western Equatorial Africa. *Science Advances*, **4**, eaar2964.
- TEAM Network (2011). Terrestrial vertebrate protocol implementation manual, v. 3.1. Trop. Ecol. Assess. Monit. Netw. Cent. Appl. Biodivers. Sci. Conserv. Int. Arlingt. VA USA.
- Tobler, M.W. (2015). Camera Base Version 1.7, User guide. Available at <http://www.atrium-biodiversity.org/tools/camera-base/> (accessed 17 September 2020).
- Vandeweghe, J.P., Christy, P., Ducrocq, M., Lee, M., Vandeweghe, G. & Pauwels, O.S.G. (2016) Biodiversité des parcs nationaux et réserves du Gabon. 2. Espèces, écosystèmes et populations, Agence nationale des parcs nationaux (ANPN), ed. edition. Libreville
- Wearn, O.R., Rowcliffe, J.M., Carbone, C., Bernard, H. & Ewers, R.M. (2013) Assessing the status of wild felids in a highly-disturbed commercial forest reserve in Borneo and the implications for camera trap survey design. *PLoS One*, **8**, e77598.
- Weckel, M., Giuliano, W. & Silver, S. (2006) Jaguar (*Panthera onca*) feeding ecology: distribution of predator and prey through time and space. *Journal of Zoology*, **270**, 25–30.
- Wickham, H. (2016) *ggplot2: elegant graphics for data analysis*. Springer.
- Willcox, D., Nash, H.C., Trageser, S., Kim, H.J., Hywood, L., Connelly, E. et al. (2019) Evaluating methods for detecting and monitoring pangolin populations (Pholidota: Manidae). *Global Ecology and Conservation*, **17**, e00539.
- Wilson, D.E. & Mittermeier, R.A. (Eds.). (2009). *Handbook of the Mammals of the World. Vol. 1. Carnivores*. Barcelona, Spain: Lynx Edicions.
- Wilson, D.E. & Mittermeier, R.A. (Eds.). (2011). *Handbook of the Mammals of the World. Vol. 2., Hoofed Mammals*. Barcelona, Spain: Lynx Edicions.
- Wilson, D.E., Mittermeier, R.A. & Lacher, T.E. (2016). *Handbook of the Mammals of the World. Vol. 6. Lagomorphs and Rodents 1*. Barcelona, Spain: Lynx Edicions.
- Ziegler, S., Fa, J.E., Wohlfart, C., Streit, B., Jacob, S. & Wegmann, M. (2016) Mapping bushmeat hunting pressure in Central Africa. *Biotropica*, **48**, 405–412.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig S1. Species average relative abundance index (RAI) of species in each placement strategy (systematic versus wildlife trail) for each area. One point represents one species, see Table 1 for species ID. Axes of RAI were square-root transformed to better visualise infrequent species,

highlighting that all areas are dominated by a few species. The bootstrap Pearson correlation coefficient (rbtp) is also displayed for each grid.

Fig S2. Dissimilarity in species composition (Bray–Curtis dissimilarity index) among camera traps (CTs) within and between placements with respect to geographic distances separating CTs in the field (0 = paired CTs, 1 = <1 km, 2 = 1–2.5 km, 3 = 2.5–5 km, 4 = 5–10 km). ‘Syst’ and ‘Trail’ indicate systematic and trail-based placement, respectively.