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Traditional shade coffee forest systems act as refuges for medium- and large-sized mammals as natural forest dwindles in Ethiopia

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ABSTRACT

Ethiopian shade coffee plantations are well documented to be bird-friendly and act as refuges for disappearing tree species. The extent to which these plantations support mammal conservation, as well as mammal sensitivity to coffee intensification, remain little studied. We studied the distribution and diversity of mammals under three coffee management systems of differing intensities (i.e., *semi-forest*, *semi-plantation*, and *plantation*) and in nearby *natural forests* in Belete-Gera Forest Priority Area, southwestern Ethiopia. We detected mammals using 30 infrared camera traps at 90 stations for a total of 4142 camera days. We used the Shannon-Wiener diversity index for diversity analysis, generalized linear mixed model for comparison of independent detection, and non-metric multidimensional scaling to show the mammalian community composition. We recorded 8815 digital videos and a total of 23 mammal species. The overall species richness, diversity, and detection of mammals did not differ between the two traditional shade coffee management systems and the natural forest but was lower in the plantation coffee system. The mammal community composition also shows variation in resilience to coffee management intensity, with primates appearing to be generally more tolerant to management intensification. We ultimately show that traditionally managed Ethiopian shade coffee farms shelter diverse mammal communities, comparable to those in nearby natural forests. Therefore, supporting traditional coffee management practices and certifying them as mammal-friendly should be implemented as strategies for the conservation of mammals, as natural forests continue to decline in Ethiopia.

1. Introduction

Protected areas contain only a small proportion of the Earth's biodiversity and are under increasing threat from human activities (Laurance et al., 2012; Jones et al., 2018). These areas alone are not enough to ensure long-term biodiversity conservation (Rodrigues et al., 2004; Chazdon et al., 2009; Mora and Sale, 2011). Hence, it is increasingly important to identify alternative management strategies and develop a multi-dimensional landscape that preserves ecosystem services, while fulfilling human needs by providing incentives for conservation outside formally protected areas (Bhagwat et al., 2008; Mora and Sale, 2011). One such promising strategy comes from agricultural systems that maintain well-structured, diverse, and dense tree canopies capable of supporting high levels of biodiversity while also providing sustainable livelihoods for the local communities and landowners (Vandermeer and Perfecto, 2007; Cassano et al., 2012; Tadesse et al., 2014b). Several studies have demonstrated that shade coffee farms planted under intact forest canopy are representative examples of such agricultural practices. Growing bodies of research have documented that these coffee farms harbor high levels of associated taxa and are important for the conservation of woody species (Tadesse et al., 2014a), amphibians (Pineda et al., 2005; Murrieta-Galindo et al., 2013), birds

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(Raman, 2006; Buechley et al., 2015; Rodrigues et al., 2018) and mammals (Williams-Guillén and Perfecto, 2010; Caudill et al., 2015; Guzmán et al., 2016; Mertens et al., 2018). However, the number and composition of taxa retained in agroecosystems depend strongly on management practices and intensity (Harvey et al., 2008; Williams-Guillén and Perfecto, 2010; De Beenhouwer et al., 2015).

Most human-modified landscapes are thus composed of a mosaic of environments with different degrees of suitability for the existence and composition of species. Long-term conservation of biodiversity depends on the ability to manage agricultural systems to meet both production and conservation goals (Harvey et al., 2008). The relative conservation value of different forms of shade coffee agriculture relates closely to management intensity (Williams-Guillén and Perfecto, 2010). So, with only a small and declining fraction of remnant forests left in such systems, including in Ethiopia where coffee likely evolved (Meyer, 1965; Anthony et al., 2002), it is important to understand the potential and limitations of shade coffee habitats to maintain large mammals. Understanding variations in communities among different habitats and the dynamics and linkages across agricultural landscape mosaics are key research priorities for conservation planning (Chazdon et al., 2009; Gardner et al., 2009).

Coffee cultivation and management in Ethiopia have a long history and production involves cultivated, semi-cultivated, or wild coffee varieties (Anthony et al., 2002). Shade tree selection is based on annual removal of understory vegetation and planting of woody species, which are preferred for shade and other purposes (Aerts et al., 2011). Based on the level of management intensity, farms exhibit variation in characteristics like tree density and diversity, species richness, shade canopy cover, and density of coffee shrubs (Hundera et al., 2013b; Tadesse et al., 2014a). As management intensity increases, the structure, composition, and diversity of plant species generally decrease (Hundera et al., 2013b). Depending on these characteristics, there are wide ranges of management systems in the area. The *semi-forest coffee* (SFC) system is cultivated mainly from wild coffee plants that regenerate spontaneously inside the forest under native tree canopies. The herbaceous understory, the shrubs, and emerging tree seedlings are slashed annually allowing natural regeneration of coffee plants (Labouisse et al., 2008; Schmitt et al., 2010; Aerts et al., 2011; Hundera et al., 2013b). The *semi-plantation coffee* (SPC) system is managed similarly to the SFC system by reducing the density of trees in the farm and selective thinning of the upper canopy and planting of preferred shade trees and coffee seedlings in open spaces (Hundera et al., 2013b). SFC and SPC are both considered traditional management systems (Hundera et al., 2013b). These traditional management systems in Ethiopia somewhat resemble the rustic coffee system in Latin America where coffee shrubs are grown under the cover of original forest canopy (Hernández-Martínez et al., 2009). However, in Ethiopia, coffee shrubs naturally occur in the understory, and coffee populations are genetically more diverse (Aerts et al., 2011; Geeraert et al., 2019). In the full *plantation coffee* (PC) system, coffee is cultivated after land clearing, systematic soil preparation, and planting of improved seedlings to increase yield and involves the planting of certain highly preferred native and exotic trees as shade. It is usually managed more intensively by continuous removal of understory vegetation and sometimes using agrochemicals (Hundera et al., 2013b; Tadesse et al., 2014a). Two other commonly practiced systems in Ethiopia are *forest coffee* and *home-garden coffee* management systems (Aerts et al., 2011).

Southwest Ethiopia maintains several of the remaining biodiversity-rich natural forests in the country and represents the major global wild habitat for Arabica coffee, *Coffea arabica* (Senbeta and Denich, 2006). The region harbors the most extensive area of shaded coffee agriculture in the country and produces the majority of the coffee nationwide. Most coffee production in the region still follows traditional coffee management regimes. However, there is increasing pressure to follow a global trend towards unshaded coffee production, connected to the increasing use of mechanized agriculture (Gove et al., 2008). Increasingly, large forested lands are being sold to investors for coffee production without any restriction on how to farm the coffee (Ango, 2018). Moreover, agricultural extension services often now recommend growing coffee with fewer shade trees to gain the highest possible yields and to be more compatible with mechanized agricultural practices (Gove et al., 2008). This phenomenon has been most profound in other coffee-growing countries like Costa Rica, Mexico, and Colombia where most of the coffee production farms experienced a high degree of shade tree reduction (Perfecto et al., 1996).

Recent studies in southwest Ethiopia have found that shade coffee farms, in which the native tree canopy is retained, harbor mammalian species similar to those in natural forests (Mertens et al., 2018). However, it is unknown how patterns of mammalian communities and their diversity change along a gradient of coffee management intensification (Rodrigues et al., 2019). Moreover, the sensitivity of different mammal species to this forest conversion to shade coffee farms is poorly understood, although differences have been found between so-called indicator species such as leopards and African civets (Mertens et al., 2018). Most mammal studies have contrasted natural forest and only one type of agroecosystem, or a variety of habitats that cannot be captured within changes in forest management complexity.

Thus, to better understand how mammalian community patterns change along a coffee intensification gradient, our study investigated the effects of coffee farm management intensification on mammalian diversity and examined the conservation potential of shade coffee agricultural systems using camera trap data in Belete-Gera National Forest Priority Area, southwestern Ethiopia. We hypothesized that the species richness, diversity, community composition, and overall detection of mammals would decline with increasing management intensity of coffee cultivation. We predicted that the SFC and SPC systems play roles in conserving medium- and large-sized mammals comparable to that of the nearby *natural forest* (NF); while the more intensively managed PC systems are of less conservation value.

Research into the effects of coffee management on mammals can have important implications for improving forest and agroforestry management. In particular, it helps to identify those species that are most sensitive to changes in forest management. Moreover, it can contribute to better understanding the tipping point, at which mammal diversity is adversely impacted by coffee management intensification. Lastly, it can provide insights to improve upon and optimize the existing criteria set for coffee certification programs (Gove et al., 2008).

2. Materials and methods

2.1. Study area

We conducted the study in Belete-Gera National Forest Priority Area (NFPA) ($7^{\circ}15'$ - 8° $45'$ N and 35° $30'$ - 37° $30'$ E) located 452 km southwest of Addis Ababa, the capital of Ethiopia (Fig. 1). We carried out all fieldwork in Gera district over 16 months from January 2017 to March 2018. The elevation of the study area ranges from 1200 to 2900 m a.s.l with steep mountainous terrain in some locations (Takahashi and Todo, 2013).

Belete-Gera NFPA occurs within the largest and most important coffee-growing region of Ethiopia. Ethiopia is Africa's largest coffee producing country and is the fifth-largest coffee producer in the world (ICO, 2019). In fact, the Ethiopian rainforest is the origin and natural reservoir of Arabica coffee (*Coffea arabica* L., Rubiaceae) (Meyer, 1965; Anthony et al., 2002). Being the origin, it is an important source for the world market of Arabica coffee (ICO, 2019), widely regarded as the finest quality coffee (Weinberg et al., 2001). Arabica coffee mainly grows as an understory shrub in forests and is the most widespread and economically valuable species in these forests (Anthony et al., 2002). In the study area, coffee grows well at altitudes ranging from 1200 to 2000 m a.s.l (Hylander et al., 2013). The study area consists of a mosaic of traditional shade coffee and coffee plantation areas and contains large

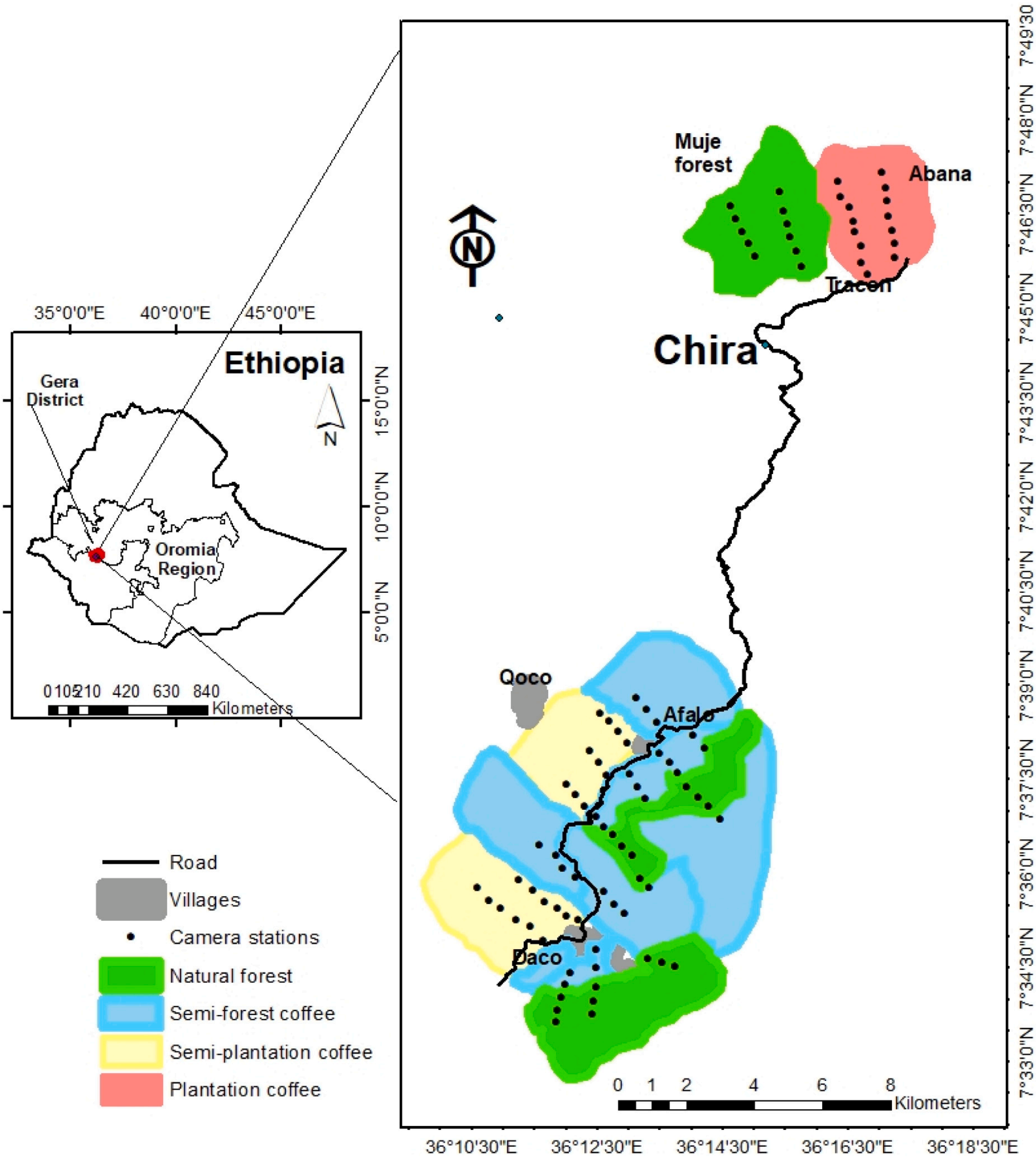

Fig. 1. Locations of camera traps in the natural forest and three shade coffee management systems at Belete-Gera NFPA, southwestern Ethiopia.

areas of Afromontane rainforest (Friis et al., 2010) in which common trees include *Olea welwitschii* (Oleaceae), *Syzygium guineense* (Myrtaceae), *Prunus africana* (Rosaceae), *Millettia ferruginea* (Fabaceae), *Croton macrostachyus* (Euphorbiaceae), *Podocarpus falcatus* (Podocarpaceae), *Cordia africana* (Boraginaceae), *Schefflera abyssinica* (Araliaceae) and *Pouteria adolfi-friedericii* (Sapotaceae).

2.2. Study design and sampling

2.2.1. Forest management system classification

We classified the study area into four forest management systems based on three easily distinguishable criteria set by Hundera et al. (2013b): undergrowth slashing, large tree cutting, and systematic planting of coffee seedlings (Fig. S1 and Table S1). To locate where each of the four forest management systems occurred in the study area, we used a combination of sources including unpublished maps (obtained from the Gera District Agricultural Office, Oromia Forest and Wildlife Enterprise, Tracon PLC, and local farmers), and ground surveys of the area in combination with informal interviews with members of the local community. We then developed a map from GPS coordinates delineating the boundaries of each forest management system in our study area using Arc Map 10.3 (Fig. 1). The SFC and SPC are considered traditional management systems while PC is a modern intensive management system (Hundera et al., 2013b). The NF consists of forested habitat characterized by an intact canopy and naturally growing plants. It is owned and protected largely by the government, though local people retain ownership of some natural forest as well.

In each of the management systems, we studied details of the vegetation characteristics, including tree density, vascular plant species richness, diversity, percentage of canopy, and ground cover (Senbeta and Denich, 2006; Hundera et al., 2013b). Vascular plants were studied using 100 plots (20 m × 20 m) laid out in the NF (n = 21), SFC (n = 42), SPC (n = 29) and PC (n = 8) systems. Plots were randomly placed near the corresponding camera station along a series of 400 m in transects spaced at 1 km apart. We counted the vascular plants, coffee plants, and estimated the percentage of tree canopy cover for each study plot. The percentage of the herbaceous ground cover was sampled in five subplots of 1 m × 1 m within each major quadrat (Senbeta and Teketay, 2003; Hundera et al., 2013b).

2.2.2. Camera-trapping

We used 30 motion-activated, digital infrared camera traps (Browning Strike Force Elite HD). Cameras were set to operate 24 h a day and to record 20 s of video per trigger. The delay between consecutive triggers was set to 1 min. Time and date were automatically recorded on each exposure. All daytime recordings were in color while during darkness, the camera produced black and white videos illuminated using infrared LEDs.

Within a 120 km^2 study area, we established transect lines ($n = 20$) and placed camera traps in each forest management system with the help of two local guides. Individual cameras were spaced 400 m apart (Mertens et al., 2018) and affixed to a tree at a height of 40–60 cm from the ground, oriented in the direction to optimize the capture of mammals. We recorded geographic coordinates, forest management system, and sampling start and end date for each camera trap. We checked cameras every 8–20 days to download videos, replace batteries, and ensure cameras were still operational. No bait was used to lure the animals to minimize the attraction of certain species to the camera. We used a rotational system for camera traps. Cameras were left in the field for 20–90 days depending on conditions the research group could not control, including malfunction of cameras and SD card capacity.

At the end of the survey period, cameras were retrieved and videos moved to storage devices. For each video, we recorded the date, time, mammal species captured, and the number of individuals and trap days. Kingdon et al. (2013) was used for mammal identifications.

2.3. Data analysis

We summarized vascular plant diversity (Shannon-Wiener index), percentage of tree canopy and ground cover, and density of coffee plants in each plot using the vegan package (Oksanen et al., 2019). We used linear modeling to estimate each of these parameters in relation to the management system (i.e., fixed effect with four levels: NF, SFC, SPC, and PC). Similarly, mammalian species richness, diversity, and evenness were calculated in R using the vegan package (Oksanen et al., 2019). Linear modeling was used to compare the diversity of mammals between the four management systems. To assess sampling completeness, we used rarefaction curves (i.e., plotting the species richness as a function of cumulative camera trap days) to check if the data collection lasted a sufficient number of days and captured (near to) the total number of species in each management system. The curves reach an asymptote when all species from the focal taxa have been recorded.

We quantified the sampling effort for each camera trap site separately by calculating the amount of camera-trap days. This is defined as the number of days the camera-trap was effectively sampling on one site (i.e., until the camera-trap was retrieved, started malfunctioning, or the SD card was full). We screened each independent mammal observation and records to derive a total set of independent detections at each site per day. Independent detection (IE) is defined as including all of the following: (1) consecutive videos of different individuals of the same or different species; (2) consecutive videos of individuals of the same species taken >30 min apart (Alvarenga et al., 2018); and (3) non-consecutive videos of individuals of the same species (e.g., five individuals in a single video would be five detections (Rich et al., 2017)).

The patterns of overall terrestrial mammal detection in the shade coffee management systems and nearby NF were compared using a generalized linear mixed model (GLMM) for independent detection, using count data with Poisson errors (Zuur et al., 2009). The number of independent detections of the overall count of mammals was taken as a response variable and forest management systems were taken as a fixed factor. We included camera stations as a random factor to account for the variation in camera trapping sites. We also controlled for differences in camera trap sampling effort by including effort (camera trap days) as an offset in the model. The analysis for primate detection including baboons *Papio anubis* was done separately using similar modeling to reduce bias due to camera traps being placed near the ground (most primate species at our study sites are arboreal). Conversely, detection of baboons, one of only two terrestrial primates in our study, was found to be very high compared with other terrestrial species. To decrease the influence of this highly abundant species, square root transformation was done for the detection of baboons.

We used non-metric multidimensional scaling (NMDS) (Clarke and Warwick, 2001) to test the effect of the coffee management system on mammalian community composition and relative abundance of camera-captured mammals. NMDS is a robust unconstrained ordination method commonly used in community ecology studies (Minchin, 1987). The Bray–Curtis dissimilarity measure was used to calculate the resemblance metric distance. The NMDS was performed on the encounter rate matrix (the number of independent events divided by sampling effort). NMDS was performed using the vegan package and function metaMDS in R (Oksanen et al., 2019). Subsequently, differences between coffee management systems were tested based on a permutation test with 999 iterations, using the function envfit (*vegan* package). In a NMDS diagram, sites that are similar in species relative abundance are located close to each other. The fit of the data was assessed by the stress value (low-stress values indicate a good fit, whereas stress values >0.3 indicate a poor fit) (Zuur et al., 2009). All analyses were done in R version 3.6.2 (R Core Team, 2019).

3. Results

3.1. Forest characteristics across different management regimes

A total of 105 vascular plant species with height > 0.5 m were recorded across the 100 plots. Average vascular plant species richness per plot was highest in the NF (16.43 ± 2.60) (mean ± SD), lower in the SFC (11.76 ± 3.13) and SPC (11.59 ± 3.27), and lowest by far in the PC (6.00 ± 3.74) management system. Percentage of canopy cover differed significantly among the NF (83.29% ± 4.54) (mean ± SD), SFC (71.07% ± 2.41), SPC (56.24% ± 4.54) and PC (34.25% ± 4.95) management systems (Fig. 2A; Table 1). Herbaceous ground cover in the SFC system (71.19% ± 4.75) (mean ± SD) was higher than in the SPC (58.65% ± 6.85) and significantly higher than in the PC management system (47.50% ± 27.51). However, no significant difference was observed in ground cover between the SFC and NF (75.71 ± 12.74) system (Fig. 2B; Table 1).

Vascular plant species diversity, here calculated as the Shannon-Wiener index, was highest in the NF (2.39 ± 0.30), lower in the SFC (2.11 ± 0.30) and SPC (2.14 ± 0.32), and lowest in the PC (1.36 ± 0.68, Fig. 2D) management system. Woody species density (individual stems/ha) was also higher in NF (2903.13/ha) than in the SFC (1735.71/ha), SPC (1554.31/ha) and PC (187.38/ha) management systems. The highest densities of coffee were recorded in the SFC (9273.81/ha) and SPC (6076.72/ha) management systems. The PC management system had 2446.88 coffee plants/ha, while the lowest density was registered in the NF (583.33/ha, Fig. 2C).

3.2. Camera trap deployments and overall capture patterns

Throughout the study period, our cameras operated for 4142 cumulative camera trap days at 90 stations (mean = 46.03 days per camera; SD ± 21.80) and recorded 8815 digital videos in total. Of these,

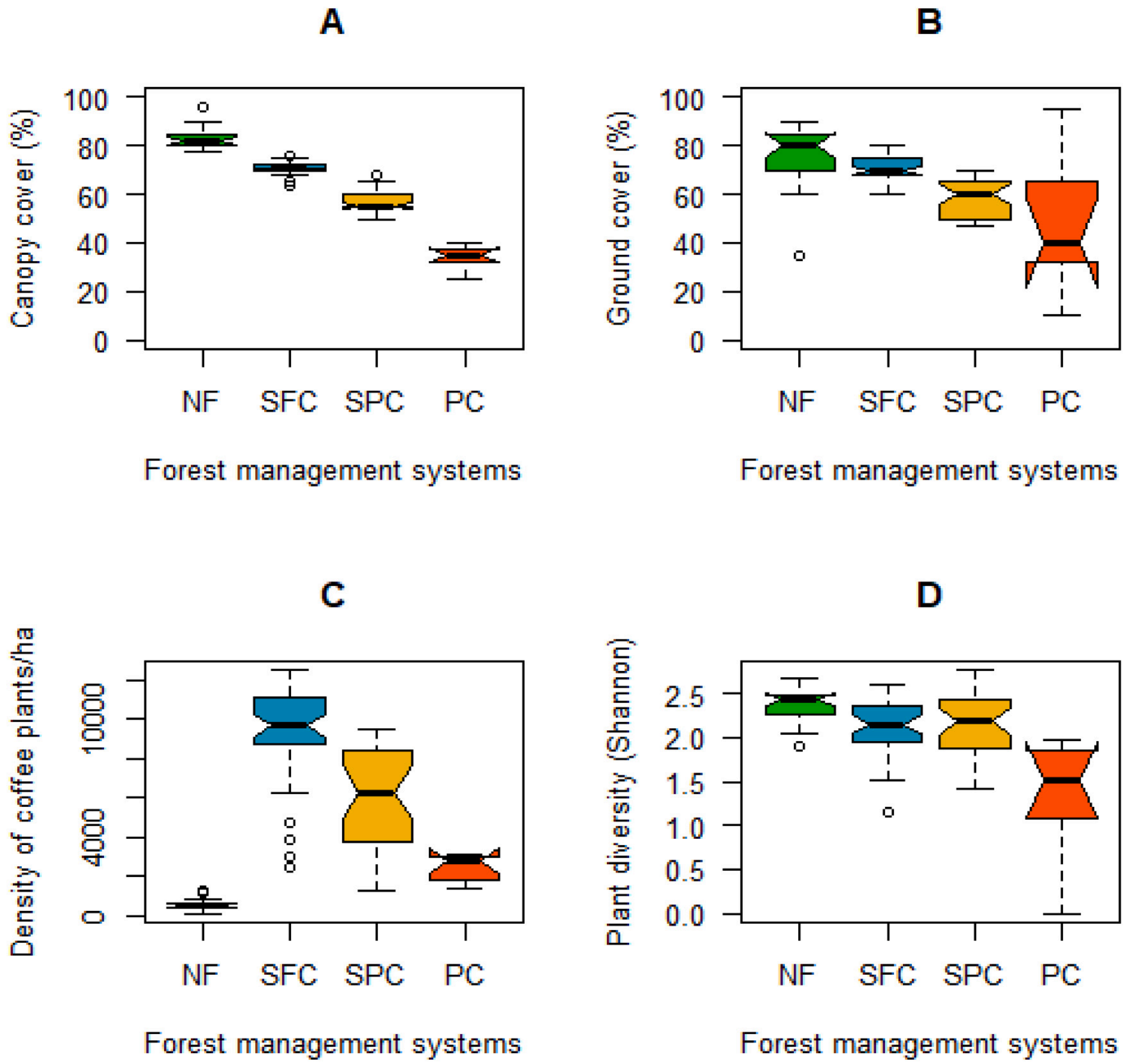

Fig. 2. Box plots showing (A) percentage of canopy cover, (B) percentage of ground cover, (C) density of coffee plants per hectare, and (D) Shannon-Wiener diversity index of woody species among the four forest management systems (natural forest, semi-forest, semi-plantation and plantation coffee) at Belete-Gera NFPA, southwestern Ethiopia.

Table 1
Estimates of parameters predicting percentage of canopy and ground cover in relation to forest management systems of fixed effect with four levels - natural forest used as a reference, semi-forest, semi-plantation and plantation coffee - at Belete-Gera NFPA, southwestern Ethiopia.

Variable	Percentage of canopy cover				Percentage of ground cover			
	Estimate	SE	t	p	Estimate	SE	t	p
Intercept	83.292	0.785	106.16	<0.001	75.7086	2.135	35.464	<0.001
Semi-forest coffee	−12.220	0.983	−12.43	<0.001	−4.518	2.676	−1.688	0.095
Semi-plantation coffee	−27.050	1.061	−25.50	<0.001	−17.053	2.886	−5.909	<0.001
Plantation coffee	−49.042	1.569	−31.25	<0.001	−28.208	4.270	−6.607	<0.001

62.5% include medium or large-sized wild mammals. Another 20.7% of videos recorded non-target species, predominantly humans (10.7%), domestic animals (cattle, sheep, goats, dogs, horses; 5.2%), birds (3.8%), insects (0.8%), and small mammals (bats, rats, squirrels; 0.1%). The remaining 16.8% of videos resulted from 'false' triggers probably caused by wind, human disturbance, leaves falling, uncaptured animal movements, or other unknown causes.

The study area maintains a diverse mammal community despite extensive habitat modification in some areas. Over the course of the study period, 23 species of mammals were recorded belonging to seven orders and 12 families (Table S2). All mammal species detected are categorized as 'Least Concern' on the IUCN Red List except the leopard *Panthera pardus* (Stein et al., 2016) and blue monkey *Cercopithecus mitis* ssp. *boutourlinii* (De Jong and Butynski, 2020), both categorized as 'Vulnerable', and the African buffalo *Syncerus caffer* (IUCN SSC Antelope Specialist Group, 2019), classified as 'Near Threatened'.

3.3. Mammal species richness and diversity

Overall mammal species richness was greatest in the NF and in the SFC system, which both contained 18 species, followed by the SPC system, which contained 16 species. The PC system was much less species-rich at only 10 species. Species rarefaction curves for all management systems show that sites placed in the intensively managed PC system yielded fewer species per unit effort than did sites in the two traditional managed coffee systems or in NF habitat. Moreover, rarefaction curves indicate that the sample size was sufficient across all management systems, reaching a plateau in most of the curves (Fig. S2).

Shannon's diversity index for mammals was highest in the SFC (1.50 ± 0.32) (mean ± SD) and NF (1.44 ± 0.24), intermediate in the SPC (1.21 ± 0.22), and lowest in the PC (0.67 ± 0.31) system (Table 2). Significant differences were found between the NF and the SPC and PC systems, but not the SFC management system.

3.4. Overall mammal detection patterns

Mammal detection strongly decreased with increasing management intensity of coffee habitats. Significant differences were obtained in the mammal detection pattern between the NF and PC management systems. No other significant differences in mammal detection were observed between management systems. The detection of primates in particular did not differ between any of the management systems (Table 3).

3.5. Community composition

Overall community composition of terrestrial mammals varied across NMDS axis 1 (explaining 50.0% of the variation) and axis 2 (explaining 26.2% of the variation; Fig. 3). The NMDS ordination produced a stress level value of 0.14.

In the ordination plot, the distribution of relative abundance across the sites indicated some clustering of species by the management system. The closer together samples occurred within the plot, the greater the similarity in their community composition. The ordination diagram showed sites in the NF clustered together with SFC with some overlap at the center showing similarity in ordinal community composition (Fig. 3A and B). Sites in the SPC and PC management systems showed a separate cluster from the NF in the first axis (Fig. 3C and D). Community composition differed significantly between the NF and the SPC ($r^2 = 0.096$, $p = 0.003$) and PC management systems ($r^2 = 0.222$, $p < 0.001$).

Of the 23 mammal species recorded across the 90 stations, only five species have consistently high encounter frequencies and can be considered abundant in all management systems (Table 4). These are olive baboons (*Papio anubis*, 98.9% of the deployments), giant forest hogs (*Hylochoerus meinertzhageni*, 82.2%), bush duikers (*Sylvicapra grimmia*, 78.9%), bushbucks (*Tragelaphus scriptus*, 75.6%) and bush pigs (*Potamochoerus larvatus*, 57.8%). Three other species (colobus monkeys *Colobus guereza*, blue monkeys *Cercopithecus mitis*, and crested porcupines *Hystrix cristata*) were also recorded in all management systems, though less frequently. Five species (warthogs *Phacochoerus africanus*, de Brazza's monkeys *C. neglectus*, blotched genets *Genetta maculata*, African civets *Civettictis civetta*, and spotted hyenas *Crocuta crocuta*) were only encountered in the NF and the two traditional coffee management systems. Three species were encountered in the NF and SFC only (African buffaloes *Syncerus caffer*, marsh mongooses *Atilax paludinosus* and leopards *Panthera pardus*). On the other hand, grivet monkeys *C. aethiops* were encountered in NF and PC only. Aardvarks *Oryteropus afer* and Senegal bushbabies *Galago senegalensis* were detected exclusively in the SFC system, whereas, Ethiopian hares *Lepus fagani* and banded mongooses *Mungos mungo* were encountered exclusively in the SPC system. Side-striped jackals *Canis adustus* were recorded only in the PC system.

Table 2
Species richness and diversity indices of medium and large mammals in natural forest (NF), semi-forest (SFC), semi-plantation (SPC) and plantation coffee (PC) at Belete-Gera NFPA, southwestern Ethiopia.

Measure	NF	SFC	SPC	PC	All sites[a]
Total number of species	18	18	16	10	23
Total camera days	1067	1148	1010	916	4142
Overall encountered	2065	1365	1147	930	5507
Independent mammals encountered	1105	1013	832	669	3619
Independent encountered per night	1.04	0.88	0.82	0.73	0.87
Shannon's diversity index[b] (±SD)	1.44 ± 0.24	1.50 ± 0.32	1.21 ± 0.22*	0.67 ± 0.31*	
Dominance	0.37 ± 0.02	0.35 ± 0.02	0.46 ± 0.03	0.69 ± 0.03	
Evenness[c]	0.24 ± 0.01	0.25 ± 0.01	0.21 ± 0.02	0.19 ± 0.02	

[a] All sites: the combination of the four management systems.
[b] Diversity is defined as $H = -\Sigma$ Pi ln Pi, where pi = proportion of capture by species i of the total sample.
[c] Evenness is defined as H/Hmax, where Hmax is the value obtained when all pi's are equal.
* significant difference.

4. Discussion

In this study, we found that two traditionally managed shade coffee systems contribute similarly to natural forests to the conservation of mammals in the Belete-Gera NFPA. This level of similarity between an agricultural system and natural forest habitat has not been reported for any other agroforestry systems, such as cacao (Cassano et al., 2012; Ferreira et al., 2020) and banana (Harvey et al., 2006) agroforests. Previously, researchers in the same region had found that shade coffee farms, in which the native tree canopy is retained, are remarkably "bird-friendly", supporting high avian diversity (Buechley et al., 2015) and act as refuges for disappearing tree species (Tadesse et al., 2014a). Here, we show that these areas also support high mammal diversity. Only in intensively managed PC farms did mammal occurrence and diversity decrease significantly relative to NF. A similar pattern has been reported for other taxonomic groups in the region, including trees (Hundera et al., 2013b), epiphytic orchids (Hundera et al., 2013a; De Beenhouwer et al., 2015), and insects (De Beenhouwer et al., 2016).

4.1. Species richness

An earlier study comparing only natural forest and managed coffee forest found that mammal species richness was similar in the two forest types, though community composition differed between them (Mertens et al., 2018). Here, studying three types of managed coffee forest and natural forest, we found that mammal species richness was comparable to that in natural forest only in the SFC and SPC management systems, while the most intensively managed system, PC, held significantly lower mammal species richness. This more nuanced result might be explained by the similarities in vegetation structure and diversity between SFC, SPC, and NF. Due to low levels of management intensity in traditional coffee farms – limited to undergrowth removal once a year at the time of harvesting (Labouisse et al., 2008; Schmitt et al., 2010; Aerts et al., 2011) and avoidance of chemical use to remove annual herbs (Buechley et al., 2015) - these systems maintain a complex vegetation composition and habitat mosaic similar to that of the NF, likely benefiting mammal species richness. In coffee plantations, intensive tree thinning and slashing of undergrowth with the repeated removal of emerging seedlings limits the potential for regeneration of wild plant species in the area (Hundera et al., 2013b), likely resulting in reduced species richness.

4.2. Mammal detection

The detections of terrestrial mammals showed no significant difference in SFC and SPC management systems compared to in NF but did

Table 3
Estimates of a generalized linear mixed model fit by the Laplace approximation (family = Poisson) predicting overall counts of terrestrial mammals and primates independent detection as a function of forest management systems at Belete-Gera NFPA, southwestern Ethiopia. Natural forest was used as a reference level for habitat categorical variable and camera station was included as a random factor.

Variable	Terrestrial mammals				Primates			
	Estimate	SE	Z	p	Estimate	SE	Z	p
Intercept	0.905	0.098	9.196	<0.001	1.002	0.080	12.496	<0.001
Semi-forest coffee	−0.172	0.113	−1.518	0.129	−0.047	0.071	−0.667	0.505
Semi-plantation coffee	−0.131	0.120	−1.095	0.274	−0.006	0.074	−0.084	0.933
Plantation coffee	−0.576	0.144	−3.998	<0.001	0.043	0.076	0.574	0.566

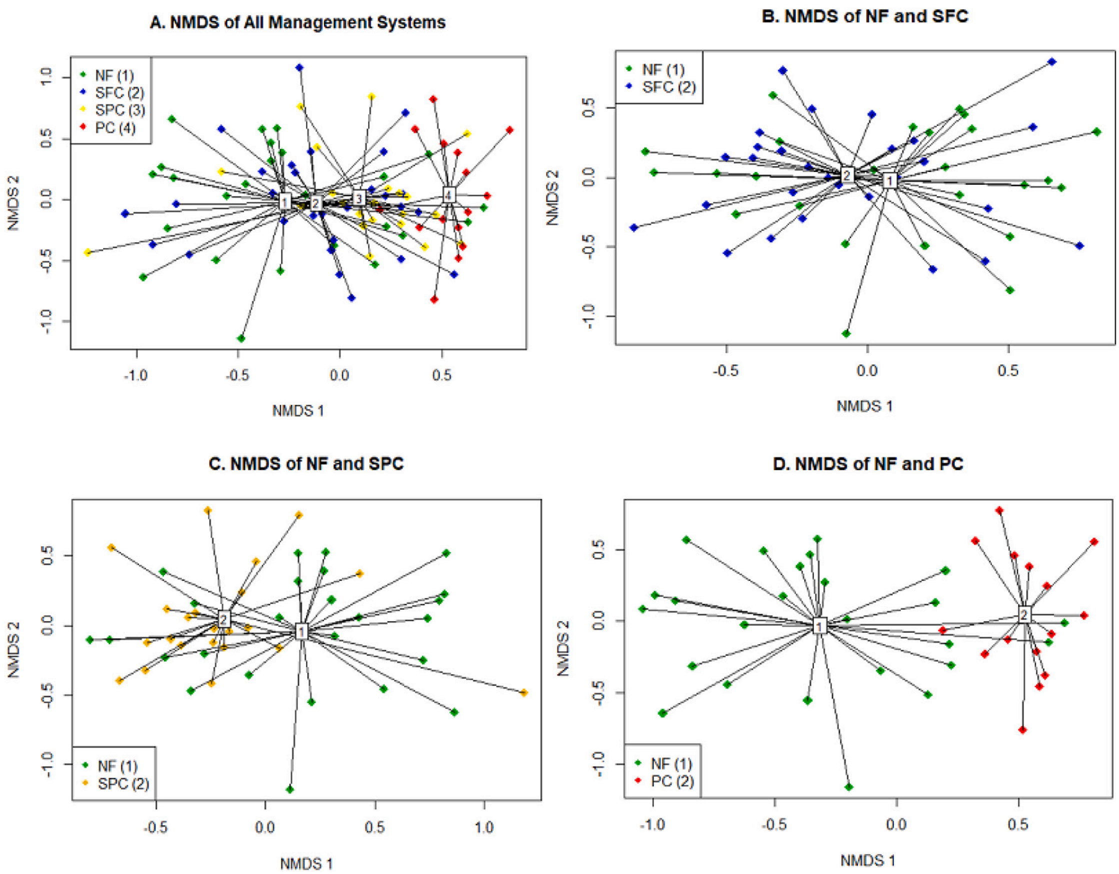

Fig. 3. Non-metric multidimensional scaling (NMDS) ordination comparing mammals among forest management systems across camera stations at Belete-Gera NFPA, southwestern Ethiopia. (A) NMDS of 90 stations in the four forest management systems combined. Colors indicate the management system: natural forest = green; semi-forest = blue; semi-plantation = yellow and plantation = red. (B), (C) and (D) are stations in the NF in relation to SFC, SPC and PC respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

differ significantly with the PC. In our study area, traditional coffee management systems are characterized by more herbaceous vegetation cover and are shown to contain higher mammal detections. Studies across the tropical world have found that mammal detection is influenced by several habitat attributes, including canopy cover and tree species diversity (Andrade-Núñez and Aide, 2010; Cassano et al., 2014) and heterogeneity of local vegetation (Kerr and Packer, 1997; Tews et al., 2004; Bali et al., 2007) as well as management intensity (Cassano et al., 2014). Patterns for all of these variables are largely determined by local management practices, creating variation in food availability (Bali et al., 2007), habitat partitioning, and obstacles for predators. The higher mammal detections in areas where there are more mature and larger shade trees suggest that mammals may benefit from the increased canopy cover and vegetation heterogeneity that traditional shade coffee management provides. These may also provide greater roosting and feeding opportunities for a variety of forest specialist large mammals (Bali et al., 2007). These might explain a higher mammal detection in the traditional management systems.

However, our results suggest that the overall detection of primates may be less affected than that of other mammals by the intensification of coffee management in the Belete-Gera NFPA. Similarly, studies in the American tropics have shown that shade coffee plantations can serve as suitable habitats for several primate species (McCann et al., 2003; Guzmán et al., 2016). This may be because coffee management intensification has more effect on the herbaceous and shrub layer than on the tree layer (Hundera et al., 2013b). Primates are unusual among mammals in occupying a wide range of habitats and niches (Chapman et al., 1999; Campbell et al., 2011). Indeed, several arboreal primate taxa found at Belete-Gera NFPA, including Boutourlini's blue monkeys (*Cercopithecus mitis boutourlini*) and Omo River black-and-white colobus monkeys (*Colobus guereza guereza*), are known from studies elsewhere in Ethiopia to be rather resilient in the face of anthropogenic disturbance to

Table 4
Summary of total independent detections of mammals categorized into high, medium and low encounter frequency with corresponding total camera trap days and number of camera deployments within each of the forest systems - natural forest (NF), semi-forest (SFC), semi-plantation (SPC) and plantation coffee (PC) - at Belete-Gera NFPA, southwestern Ethiopia.

Encounter		Deployments[a]						Total independent detections[b]				
		Stations						Camera days				
		25	28	22	15	90		1067	1148	1010	916	4142
	Species	NF	SFC	SPC	PC	Total	%	NF	SFC	SPC	PC	Total
High	Olive Baboon *Papio anubis*	25	27	22	15	89	98.9	1726	1099	1179	1148	5152
	Giant forest hog *Hylochoerus meinertzhageni*	21	26	20	7	74	82.2	461	362	224	15	1062
	Bush duiker *Sylvicapra grimmia*	16	22	18	15	71	78.9	125	203	184	191	703
	Bushbuck *Tragelaphus scriptus*	19	23	18	8	68	75.6	192	123	70	17	402
	African buffalo *Syncerus caffer*	17	5	0	0	22	24.4	297	8	0	0	305
	Bushpig *Potamochoerus larvatus*	21	15	11	5	52	57.8	94	96	37	17	244
	Warthog *Phacochoerus africanus*	6	7	5	0	18	20.0	11	55	67	0	133
	Colobus monkey *Colobus guereza*	2	7	5	2	16	17.8	9	16	10	8	43
Medium	De_Brazza's_monkey *Cercopithecus neglectus*	5	8	1	0	14	15.6	15	20	3	0	38
	Blue monkey *Cercopithecus mitis boutourlinii*	4	4	6	2	16	17.8	7	11	9	2	29
	Spotted hyena *Crocuta crocuta*	4	2	2	0	8	8.9	21	2	2	0	25
	Blotched genet *Genetta maculata*	6	3	1	0	10	11.1	13	6	1	0	20
	African civet *Civettictis civetta*	3	5	2	0	10	11.1	3	8	2	0	13
	Grivet monkey *Cercopithecus aethiops*	3	0	0	1	4	4.4	9	0	0	3	12
	Crested porcupine *Hystrix cristata*	3	2	1	1	7	7.8	4	2	1	2	9
	Marsh mongoose *Atilax paludinosus*	5	2	0	0	7	7.8	5	2	2	0	9
	Leopard *Panthera pardus*	3	2	0	0	5	5.6	3	2	0	0	5
Low	Aardvark *Oryteropus afer*	0	2	0	0	2	2.2	0	3	0	0	3
	Side-striped jackal *Canis adustus*	0	0	0	2	2	2.2	0	0	0	3	3
	Ethiopian Hare *Lepus fagani*	0	0	2	0	2	2.2	0	0	2	0	2
	Senegal Bushbaby *Galago senegalensis*	0	1	0	0	1	1.1	0	2	0	0	2
	Banded_mongoose *Mungos mungo*	0	0	1	0	1	1.1	0	0	1	0	1
	White-tailed mongoose *Ichneumia albicauda*	1	0	0	0	1	1.1	1	0	0	0	1
	Sum							2996	2020	1794	1406	8216

[a] Total number of camera deployments (locations) in which a species was observed.
[b] Total number of independent species detections per forest management system.

their habitats (Tesfaye et al., 2013, 2021; Rodrigues et al., 2021).

4.3. Mammal community composition

The community composition of mammals showed similarity between the SFC and NF but differed across a gradient to the SPC and PC management systems. Such community similarities have not been reported previously in other types of agricultural systems (Harvey et al., 2006; Cassano et al., 2012; Ferreira et al., 2020). However, the shift in mammal composition along a gradient of management intensity documented here is consistent with other studies where coffee agriculture hosts distinct mammalian communities compared to natural forests (Daily et al., 2003; Caudill et al., 2015; Mertens et al., 2018).

In our study, the sensitivity of some forest specialists with increasing coffee management intensity has been observed in the SPC and PC management systems. For instance, species like African buffaloes and leopards were encountered repeatedly in the NF and SFC areas but were not recorded in the SPC or PC management systems. The SFC system could play a critical role as a corridor and an alternative habitat for these forest specialists. Some species are more sensitive and prefer dense or undisturbed forest habitats with limited human interference (Urquiza-Haas et al., 2009). For instance, species like African buffalo could be increasingly hunted in more intensively managed habitats (Laurance et al., 2006) and decline due to habitat disturbance and insufficient grazing areas (Bennitt et al., 2014). Similarly, a decline in prey abundance with increased management intensity could affect the number and survival of carnivores including leopards and African civets (Mertens et al., 2018; Rodrigues et al., 2019).

4.4. Implications for conservation and conclusions

As natural forest habitat continues to decline in the Belete-Gera NFPA (Hylander et al., 2013; Todo and Takahashi, 2013; Ango et al., 2020), this study shows that traditional shade coffee farming management, with its greater canopy cover and vegetation heterogeneity appears to better support mammals than the intensive PC system increasingly being implemented in the region (Ango, 2018). Our results build on the growing evidence of different studies from around the tropics that, if correctly implemented, shade coffee agriculture can provide additional opportunities for the conservation of mammals and other native wildlife (Perfecto and Armbrecht, 2003; Bali et al., 2007; Estrada et al., 2012; Mertens et al., 2018). In several coffee-growing countries, it has been reported that shade coffee agriculture acts as a potential buffer around protected areas, and serves as an extension of large mammal habitat and distribution corridors (Bali et al., 2007). These properties of shade coffee agriculture have the potential to benefit not only the local ecology and biodiversity but also the economy of the local farmers.

The forested lands in southwestern Ethiopia are remnant Afromontane rainforest (Friis et al., 2010), with the majority used for coffee agriculture. Most of these lands are traditionally managed and owned by private individuals (Hundera et al., 2013b). Because the conservation of native forest remnants is dependent upon the positive attitudes of the surrounding land-users, providing local farmers with a sustainably harvested resource may be the best way to ensure the longevity of the forest. One of the practices that offer an opportunity to link ecological and economic goals in agricultural areas is coffee habitat certification (Ibanez and Blackman, 2016; Takahashi and Todo, 2017). In different countries, conservation efforts open up an opportunity to implement initiatives that benefit the local biodiversity and the local communities by integrating coffee management with certification. This can be achieved through providing a better price for the coffee, reducing the threats to biodiversity by protecting the remaining natural forest from the direct effects of more intensive agriculture and higher-density human settlements, thus enhancing the survival prospects of species in the region. Therefore, certifying and publicizing traditional shade coffee as "mammal-friendly" has the potential to increase the incomes of smallholder coffee farmers. This strategy would provide them with a strong incentive to maintain traditionally managed farms instead of intensifying into monoculture coffee plantations that are poor for biodiversity conservation (Gove et al., 2008; Takahashi and Todo, 2017).

The current criteria used for the coffee sustainability certification schemes by the Rainforest Alliance and Smithsonian Bird Friendly organizations mainly emphasize vegetation complexity, including the maintenance of shade tree composition, structure, tree height, density, number of strata in the canopy, and percentage of canopy cover (Philpott et al., 2007). Furthermore, most certifications, on which these farm management protocols are based focus on insect and bird communities (Gordon et al., 2007). So far, mammals are not considered for these certification criteria. Since many mammals are sensitive to habitat disturbance gradients (Wallgren et al., 2009), they can be used as "early warning" indicators for environmental changes (Burthe et al., 2016). However, there is hardly any awareness of this issue in the world coffee market. Therefore, developing a special certification type for these areas, including mammal diversity among the criteria, could be important for better conservation of the habitat and the biodiversity in coffee-growing areas. Wiersum et al. (2008) suggested an "area-based" certification approach for Ethiopia focusing on the sustainable management of overall landscapes that can operate at a scale most conducive to certification of a large number of smallholder farmers. It is, however, important to recognize that these coffee systems cannot fully replace the natural forests as a habitat, particularly for more specialized mammals like African buffaloes and leopards. Therefore, a balanced landscape mosaic of traditional coffee farms and extensive areas of the remnant natural forest may be a winning combination for the conservation of mammalian species in the Belete-Gera NFPA. Accordingly, supporting, certifying, and promoting the traditional coffee management practices and ensuring that farmers receive a reasonable price for their commodities are an approach that should be considered as a conservation strategy in coffee-growing areas where the natural forest is dwindling.

CRediT authorship contribution statement

BE, AA and NCS designed the research; BE collected field data; BE, DT and AA analyzed the data; BE, AA, PJF, DT, AB, MDB, KH, LL and NCS wrote the paper. All the authors approved the submission of this paper.

Declaration of competing interest

The authors declare no conflicts of interest.

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Ethical statement

The research used non-invasive, unbaited, remotely set motion-activated camera traps and hence did not involve direct contact with the animals. Permission was issued from the Ethiopian Wildlife Conservation Authority, Oromia Forest and Wildlife Enterprise, and Gera District office.

Appendix A. Supplementary data

Supplementary information to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109219.

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