Original study

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Season and habitat affect diversity, abundance and reproductive state of small mammals near Lake Abaya, Ethiopia

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Abstract: This study investigated the spatio-temporal association of small mammals in human-modified habitats. Small mammals were sampled using Sherman traps along 200 m transects (with one trap at every 10 m interval) in each of four habitats (cropland, forest patch, scrubland and wetland) replicated twice. Additional trapping was carried out in rural settlements comprising of eight homesteads, with five traps per homestead. Trapping was conducted in three sessions during the agricultural seasons: rainy (October), off-rain (December) and dry (February) over two years (2018 and 2019). In each session, trapping was carried out for three consecutive nights. A total of 497 small mammals belonging to 12 species from four families (Soricidae, Macroscelididae, Gliridae and Muridae) were captured. Murine rodents accounted for 99.4% of the animals with *Mastomys erythroleucus* (58%) being the dominant species. The scrubland had the highest small mammal species diversity while the cropland had the lowest. *M. erythroleucus* was not strongly associated with any spatio-temporal parameter and scored majority of seasonally reproducing individuals in the cropland, signifying its pest importance. Though disconnected from protected areas, habitats such as the scrubland harbor diverse small mammal species (including a vulnerable-endemic species, *Grammomys minnae*), suggesting the habitats' significance for ecosystem functioning and conservation.

Keywords: declining biodiversity; Ethiopia; habitat association; land-use/cover changes; small mammals.

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1 Introduction

Anthropogenic ecosystem changes are intensifying due to rapid population growth and unsustainable resource use worldwide (Western 2001). However, it has been argued that conservationists often focus on protected areas with limited appreciation of landscape-scale effects (Donaldson et al. 2016; Reed et al. 2017). Consequently, agricultural landscapes that are often close to protected areas remain disconnected from protected area management. Such an approach may exacerbate biodiversity loss that underpins ecosystem services such as biological pest control (Labuschagne et al. 2016) and zoonoses regulation through the dilution effect (Luis et al. 2018).

Among the biodiversity hotspots in Ethiopia (Abebe 2010), the Abaya-Chamo Basin (ACB) in the Ethiopian Rift Valley has suffered severe anthropogenic land use/cover changes in past decades (Ashebir et al. 2018). For example, extensive areas west of Lake Abaya were cleared in the 1960s and 1970s for cotton monoculture (Zerihun and

Yeshitila 2003), attracting the attention of ecologists attempting to understand how such changes have affected the distribution of fauna and flora. Most of these studies have focused on the adjacent Nech Sar National Park (Fetene et al. 2019; Simon et al. 2020), with little attention to the habitats surrounding conservation areas, particularly agricultural landscapes.

In Ethiopia, ecological studies on small mammals have typically aimed at describing endemism and new taxa from forests and mountain ecosystems (Afework 1996; Bryja et al. 2019b; Craig et al. 2020; Lavrenchenko et al. 2016; Yalden et al. 1996). This is due to the fact that most of the mammalian endemism of Ethiopia is concentrated in highlands, with few exceptions such as *Mastomys awashensis*, which typically prefers lowland systems (Lavrenchenko and Afework 2017). However, there is a lack of information on the ecology of small mammals in lowland agricultural systems with the view of managing problematic, endemic and invasive species to help conserve beneficial and at risk species. This is important as some taxa in the ACB are likely to suffer local extinction before they are properly identified (Lavrenchenko and Afework 2017). Small mammals are useful indicators of ecosystem integrity (Auffray et al. 2009; Avenant 2011). Anthropogenic defaunation causes reduction in small mammal biodiversity but increases the density of opportunistic species that can occur as pests in agriculture and are carriers of infectious diseases (McCauley et al. 2015; Young et al. 2014). Evidence also suggests that changes in land use/cover and climate can have synergistic effects in structuring small mammal assemblages (Young et al. 2017). Moreover, in protected areas, megafauna such as elephants and giraffes are known to negatively impact small mammal communities (McCleery et al. 2018), further supporting our focus on small mammals outside of protected areas.

Earlier surveys (Demeke et al. 2007; Sintayehu et al. 2011) in the ACB were limited to the Nech Sar National Park and the nearby state-owned maize and cotton plantations and focused on small mammal species composition and a few population parameters of the small mammals. The authors neither investigated how the different anthropogenic habitats (including homesteads) and seasons (including the off-rain season) affect the distribution, diversity, habitat association and reproductive state of small mammals, nor applied genetic approaches which are vital to identify cryptic small mammal diversity (Bryja et al. 2019b; Lavrenchenko and Afework 2017). Therefore, the objective of this study was to investigate the effect of contrasting anthropogenic habitats and seasons on diversity, abundance, habitat association, age–sex structure and reproductive activities of small mammals in a human-modified landscape adjacent to Lake Abaya, Ethiopia.

2 Materials and methods

2.1 Study area

Chano (6°4′0″N, 37°37′0″E, ~1200 m above sea level, area = 6674 ha) is part of the ACB, located 15 km north of Arba Minch town adjacent to the western shore of Lake Abaya in Southern Ethiopia (Figure 1). Chano is divided into three rural villages namely; Chano Chalba (CC), Chano Mile (CM) and Chano Dorga (CD). Rainfall is bimodal with short rains in September-November and the long rains from March to May (Degife et al. 2019). The area receives annual rainfall ranging from 800 to 1200 mm. The average annual maximum and minimum

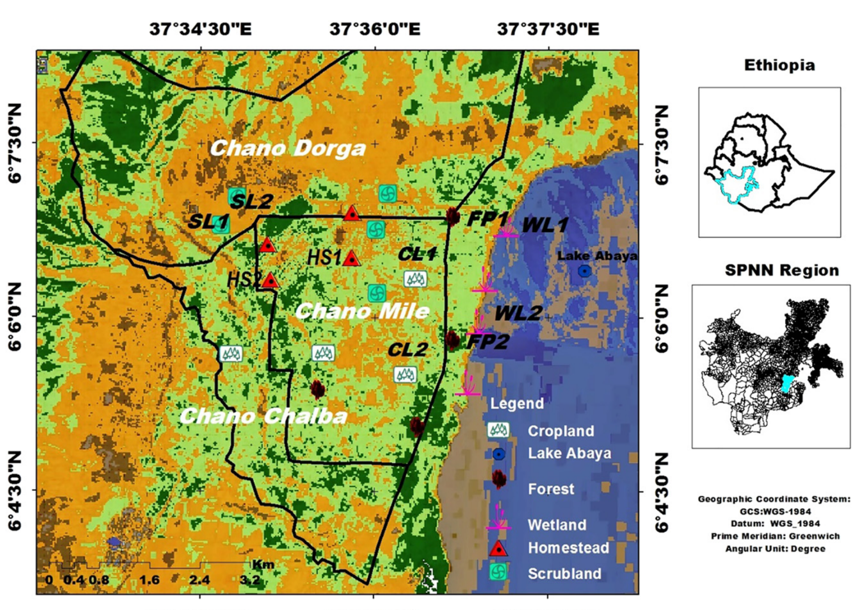

Figure 1: Map of the study area showing the habitats considered for small mammal sampling: WL1 and WL2 = wetland sampling sites one and two; FP1 and FP2 = forest path sampling sites one and two; CL1 and CL2 = cropland sampling sites one and two; SL1 and SL2 = scrubland sampling sites one and two and HS1 and HS2 = homestead sampling sites one and two.

temperatures are 30 and 17 °C, respectively (Clark 2010). The ecosystem of Chano is composed of a mosaic landscape consisting of patches of bushland, wetland, agricultural land and rural settlements. The proportions of our target sites (data from our unpublished supervised land use/cover classification) are indicated below.

The cropland accounts for 23.1% of the area, with average ownership per household being 1.14 ha, of which 63 and 37% are allotted for cultivation of cash crops (primarily banana) and maize (*Zea mays* L.), respectively (see Zewdneh et al. (2020) for a detailed description). Maize is the staple crop and is cultivated during the short rains' cropping season between August and December. The rainfed agriculture is supplemented with small-scale irrigation from the Hare River at times of rainfall shortage or fluctuation (Roy et al. 1999). Individual croplands are separated by hedges (often composed of disturbance affiliated shrubs such as *Lantana camara* and *Acalypha fruticosa* (Yonas et al. 2020) which are used as fences and barriers to people and livestock but can also harbor rodent pests (Jacob 2008). Abandoned farmlands (due to soil salinity or waterlogging (Tuma 2007)) and the banks of irrigation canals (Roy et al. 1999) are also suspected to harbor small mammals.

The forest patch covers 14.3% of the area and is characterized by few mature trees including; *Ficus vasta, Crateva adansonii* and *Trichilia emetica*, with forest edges covered by shrubs such as *A. fruticosa*. The forest patch suffers severe degradation due to ongoing clearance for banana plantation (including in buffer zones of Lake Abaya), seasonal flooding from upland areas, embedment by sediment displaced water from Lake Abaya, livestock overgrazing and unsustainable resource extraction (Ashebir et al. 2018).

The scrubland accounts for 21.0% of the area and is characterized by Acacia woodland vegetation type (Mengesha et al. 2020) interspersed with *A. fruticosa* (Yonas et al. 2020).

The wetland contributes 29.3% of the area and is characterized by macrophytes particularly, *Cyperus* spp. and *Aeschynomene elaphroxylon*, which is locally used for construction of traditional boats (Dikaso 2013). Sediment-displaced water from Lake Abaya increases the overall size of the wetland (Ashebir et al. 2018) while the wetland at the western shore of Lake Abaya is threatened with invasive water hyacinth (*Eichhornia crassipes*) (Bedilu et al. 2017).

The homesteads (rural houses and surrounding peri-domestic area) account for 12.5% of the area. A typical homestead has an area of about 1000 m^2 and comprises of three houses (often made of mud-plastered wood constructed walls, an earth floor and corrugated iron roofing). Domestic livestock (cattle, goats, sheep and donkeys) are often kept in separate pens in household-compounds. Harvested cereals, particularly, shelled maize grains are stored indoors in woven polyethylene bags or metal/clay containers of various sizes. The house and peri-domestic areas are fenced with trees and other plants including *A. fruticosa* and *Jatropha curcus*. Homegardens are planted with various fruit and non-fruit trees including; *Mangifera indica, Persea americana, Carica papaya, Annona cherimola, Citrus aurintifolia, Moringa stenopetala, Coffea arabica, Cordia africana, Trichillia emetica, Croton macrostachyus, Kigelia ethiopicum, Ehretia cymosa* and *Commiphora africana* (Aynalem et al. 2020).

2.2 Small mammal sampling

Removal trapping was conducted in two 200 m permanent transect lines (one in each of the replicate habitats: cropland, forest-patch, scrubland and wetland), each with 20 trap stations, 10 m apart, with one Sherman live trap (7.5 × 9.0 × 23.0 cm, HB Sherman Trap Inc. Tallahassee, USA) per trapping station. Forty Sherman traps were set in eight homesteads with five traps per homestead (four from each of the CM and CC villages). In each homestead, the setup of the traps comprised two inside the house (bedroom and near food stores) and three outside the house (near gardens and around live-fencings or piles of wood/stone) (Aplin et al. 2003). The homesteads were selected based on presence of live-fencings, absence of domestic rodent predators (cat and/or dog) and no rodenticide application. The four habitats and eight homesteads were approximately 500 m apart. The transect lines were set along sections of the habitats with structures that small mammals may use for nesting or as foraging runways. The direction of the transect lines followed that of the drainage line of the area, west to east. Traps were baited with peanut butter mixed with maize flour. Trapping took place three times over the agricultural seasons: rainy (October), off-rain (December) and dry (February) over two years (2018 and 2019), with three consecutive days of trapping per trapping session. Traps were inspected for captures early in the morning and late in the afternoon in order to capture diurnal and nocturnal species.

The three agricultural seasons considered for small mammal sampling vary significantly with their average monthly rain fall and temperature (data for the years 1983–2016 from National Meteorological Agency of Ethiopia). The seasons also represent the different periods in maize cultivation with young maize plants, maize at harvesting stage and fallow fields characterizing the area during rainy, off-rain and dry seasons, respectively. From our field observation, the area is also characterized by higher abundance of sprouting herbs during the rainy season followed by fruiting/seeding of the herbs during the off-rain season and dying of the herbs during the dry season.

2.3 Processing of captured small mammals and sample collection

The captured small mammals were sacrificed by cervical dislocation prior to dissection following the guideline by Sikes et al. (2016), sexed, weighed (using a Pesola spring balance, accurate to the nearest g), and standard external measurements (lengths of the head–body, tail, hind foot and ear) were taken. In the field, the animals were identified to genus level following Happold (2013), Happold and Happold (2013), Kingdon et al. (2013) and Bryja et al. (2019b). Females with closed vagina were recorded as reproductively inactive while females with perforated vagina, pregnant, lactating or with scars in the uterus were recorded as reproductively active. Males with abdominal testes were considered as reproductively inactive while males with scrotal testes were categorized as reproductively active. Approximate ages (adult, sub-adult and juvenile) were determined based on weight, pelage color, external measurements and sexual maturity (Aplin et al. 2003). A liver sample was taken from each individual, preserved in 96% ethanol and stored at −20 °C for use in cytochrome *b* DNA genotyping. Animal carcasses were preserved in 70% ethanol and stored at the zoology laboratory of the Arba Minch University, Ethiopia.

2.4 Molecular species confirmation

Species of the captured small mammals were confirmed with a polymerase chain reaction (PCR) targeting the mitochondrial gene for cytochrome *b* (*CYTB*) at the Evolutionary Ecology Group Laboratory of the University of Antwerp, Belgium. DNA was extracted by NucleoSpin® Tissue kit (Macherey-Nagel®, Filterservice-Belgium, art.n° 740952.250) and the mitochondrial gene for *CYTB* was sequenced following the protocols in Bryja et al. (2014).

2.5 Data analysis

Trap-nights were calculated from the number of traps multiplied by the number of nights they were active. Trap success was calculated by the formula:

$$\textbf{Trap Success}(\%) = \frac{\textbf{Number of captures}}{\textbf{Number of trap nights}} \times \mathbf{100}.$$

The total number of different species in each habitat was used as species richness (**S**).

Shannon's diversity index was calculated with the formula:

$$H' = -\sum p_i ln(p_i).$$

where p_i is proportional representation of species i and ln is the natural logarithm of the number. The transformed Shannon's index was calculated using the formula, $e^{H'}$ where **'*e*'** is the exponential, which was used since it is linear and more intuitive for comparing the different habitats than the non-linear untransformed index (Jost 2006). Shannon evenness indices showing how the species were distributed in a community were calculated for each habitat by the formula:

$$E = H'/lnS$$

where, E is the evenness index, H' is the Shannon's diversity index, S is the species richness and ln is the natural logarithm (Fichet-Calvet et al. 2009). A non-metric multidimensional scaling (NMDS; Euclidean distance similarity measure) was performed using metaMDS function on the number of individual small mammal species from each of the habitat types during the rainy, off-rain and dry seasons to illustrate the correlation between the occurrence of small mammals and the spatio-temporal settings. The goodness-of-fit of the NMDS ordination was measured using standardized residual sum of squares (stress). Chi-square tests were used to establish the association of habitat and season with the distribution, age–sex structure and reproductive activities of the small mammals. Statistical analyses were performed using the R version 3.5.3 (R Development Core Team 2019).

3 Results

3.1 Small mammal abundance and diversity

An aggregate sampling effort of 3600 trap-nights (720 per habitat) resulted in capturing 497 small mammal individuals belonging to 12 species under four families: Soricidae (represented by *Crocidura* sp. (Yabelo-Serengeti) (according to comparison with existing sequence database at the Institute of Vertebrate Biology, Czech Academy of Sciences) and *Crocidura olivieri*), Macroscelididae (represented by *Elephantulus rufescens*), Gliridae (represented by *Graphiurus* sp. "C") (sensu Bryja et al. 2019b) and Muridae (represented by *Mastomys erythroleucus*, *Acomys percivali*, *Arvicanthis niloticus* "C2–C4" (sensu Bryja et al. 2019a), *Gerbilliscus phillipsi*, *Lemniscomys macculus*, *Mus minutoides*, *Rattus rattus* and *Grammomys minnae*).

The rodents and insectivores accounted for 95.6 and 4.4% of the total captures, respectively. The family Muridae accounted for 99.4% of the rodent assemblage. Moreover, 58.3% of the murine rodents belonged to *M. erythroleucus*. The abundance of the rodents was the highest for the cropland (34.0%) followed by the forest patch (24.4%), scrubland (20.6%), homestead (10.7%) and wetland (10.3%) (Table 1). However, the cropland was the lowest in small mammal species diversity (transformed H' = 2.6) and evenness (E = 0.48) while the scrubland was the highest in these indices (transformed H' = 4.5; E = 0.75) (Table 2).

The distribution of small mammal species varied significantly with habitat types (χ^2 = 426.87, df = 44, p < 0.001) and seasons (χ^2 = 36.93, df = 22, p < 0.05). *M. erythroleucus* was the most common and dominated numerically in nearly all the habitats (Table 1). Cropland scored the highest proportion of *M. erythroleucus* (42.2%) followed by the forest patch (24.4%), scrubland (18.2%), wetland (11.6 %) and homestead (3.6%). *M. erythroleucus* also scored the highest proportion in the rainy season (42.9%) followed by the off-rain (32.4%) and dry (24.7%) seasons. *M. minutoides* was the second most frequent rodent across the different habitats. Thirty-five percent of all captured *M. minutoides* were trapped in the cropland followed by the homestead (28.2%), forest patch (19.7%), scrubland (11.3%) and wetland (5.6%). The rainy season contributed the highest proportion (39.4%) of *M. minutoides* followed by the dry (33.8%) and off-rain (26.8%) seasons. *A. niloticus* ranked third in the frequency of rodent occurrence across the different habitats. Wetlands contributed the highest proportion (32.0%) of *A. niloticus* while it was represented in equal proportions in the cropland and scrubland. The dry season scored the highest proportion (43.9%) of *A. niloticus* followed by the rainy (31.7%) and off-rain (24.4%) seasons. Moreover, the proportions of the different small mammal species varied significantly between the years of sampling (χ^2 = 40.30, df = 11, p < 0.001). *M. erythroleucus* and *A. niloticus* scored higher proportions in year two (between October 2019 and February 2020) than in year one (between October 2018 and February 2019).

3.2 Spatio-temporal association of the small mammals

The non-metric multidimensional scaling (NMDS) plot (Figure 2) illustrated the association of small mammal

Table 1: Small mammal composition and abundance according to the habitat types and seasons (S1 = rainy, S2 = off-rain, S3 = dry) in the agricultural landscape adjacent to Lake Abaya, Ethiopia.

Species	No. (%) in cropland			No. (%) in forest patch			No. (%) in scrubland			No. (%) in wetland			No. (%) in homestead			Overall no. (%)
	S1	S2	S3	S1	S2	S3	S1	S2	S3	S1	S2	S3	S1	S2	S3	
Rodents																
Mastomys erythroleucus	42 (15.3)	43 (15.6)	31 (11.3)	31 (11.3)	27 (9.8)	9 (3.3)	27 (9.8)	8 (2.9)	15 (5.5)	15 (5.5)	9 (3.3)	8 (2.9)	3 (1.1)	2 (0.7)	5 (1.8)	275 (55.3)
Mus minutoides	8 (11.3)	4 (5.6)	13 (18.3)	9 (12.7)	4 (5.6)	1 (1.4)	2 (2.8)	3 (4.2)	3 (4.2)	1 (1.4)	1 (1.4)	2 (2.8)	8 (11.3)	7 (9.9)	5 (7.0)	71 (14.3)
Arvicanthis niloticus	5 (12.2)	3 (7.3)	4 (9.8)	3 (7.3)	0	0	1 (2.4)	5 (12.3)	6 (14.6)	4 (9.8)	1 (2.4)	8 (19.5)	0	1 (2.4)	0	41 (8.2)
Lemniscomys macculus	0	0	0	10 (34.5)	8 (27.6)	11 (37.9)	0	0	0	0	0	0	0	0	0	29 (5.8)
Rattus rattus	0	1 (5.3)	0	0	0	0	0	0	0	0	0	0	4 (21.1)	7 (36.8)	7 (36.8)	19 (3.8)
Acomys percivali	3 (16.7)	0	3 (16.7)	1 (5.6)	0	2 (11.1)	1 (5.6)	3 (16.7)	5 (27.8)	0	0	0	0	0	0	18 (3.6)
Gerbilliscus phillipsi	0	0	0	0	0	0	6 (33.3)	5 (27.8)	7 (38.9)	0	0	0	0	0	0	18 (3.6)
Graphiurus sp.C	0	0	1 (33.3)	0	0	0	0	0	0	0	0	0	2 (66.7)	0	0	3 (0.6)
Grammomys minnae	0	0	0	0	0	0	1 (100)	0	0	0	0	0	0	0	0	1 (0.2)
Insectivores																
Crocidura sp. (Yabelo-Serengeti)	0	0	0	0	4 (30.8)	1 (7.7)	2 (15.4)	4 (30.8)	1 (7.7)	0	0	0	0	1 (7.7)	0	13 (2.6)
Crocidura olivieri	0	1 (14.3)	0	0	0	2 (28.6)	1 (14.3)	0	0	1 (14.3)	0	2 (28.6)	0	0	0	7 (1.4)
Elephantulus rufescens	0	0	0	0	0	0	0	0	2 (100)	0	0	0	0	0	0	2 (0.4)
Total capture			162			123			108			52			52	497

Table 2: Trap success (*TS*) and diversity indices (*S* = species richness; *H′* = Shannon's diversity index; *E* = evenness) of small mammals according to the different habitats in the agricultural landscape adjacent to Lake Abaya, Ethiopia.

Parameter	Habitat					Overall
	Cropland	Forest patch	Scrubland	Wetland	Homestead	
TS (%)	22.5	17.1	15.0	7.2	7.2	13.8
S	7	7	9	4	6	12
H′	0.94	1.30	1.64	1.0	1.33	1.56
Transformed *H′*	2.6	3.5	4.5	2.7	3.6	4.2
E	0.48	0.66	0.75	0.73	0.74	0.62

species with spatio-temporal parameters. *M. erythroleucus* was not strongly associated with any of the spatio-temporal settings and hence can be considered as opportunistic. *A. niloticus* appeared to be associated more with the cropland and wetland habitats in the three seasons. *Graphiurus* sp. "C" was strongly and *M. minutoides* was weakly associated with the homestead and more likely to co-occur in this habitat during the dry season. *L. macculus* and *C. olivieri* were associated with forest patch and more likely to co-occur in this habitat during the dry season. *A.percivali*, *E. rufescens*, and *G. phillipsi* were associated with the scrubland and more likely to co-occur in this habitat during the dry season. *G. minnae* was limited to scrubland habitat during the rainy season. *R. rattus* was almost exclusively associated with the homestead during the three seasons. The species is likely to co-occur in the homestead habitat with *Graphiurus* sp. "C" during the rainy season.

3.3 Sex and age structure of the small mammals

All the rodent species had male biased sex ratios, except *G. phillipsi* and the two shrew species which were female biased ($\chi^2 = 24$, df = 12, $p < 0.05$) (Figure 3). The dominant species (*M. erythroleucus*) scored male: female sex ratios of 1.23:1, 1.79:1, 1.08:1, 0.52:1 and 0.43:1 in the cropland, forest patch, scrubland, wetland and homestead, respectively ($\chi^2 = 10.17$, df = 4, $p < 0.05$).

The large majority of the small mammal individuals were adults ($n = 452$) followed by sub-adults ($n = 44$) and juvenile ($n = 1$), with *M. erythroleucus* numerically dominating all age classes (Figure 4). Considering specific seasons, the dry season contributed the lowest count ($n = 130$) of adult individuals while it contributed the highest counts for sub-adult ($n = 23$) and juvenile ($n = 1$) ($\chi^2 = 17.35$, df = 4, $p < 0.01$). Similarly, the population of *M. erythroleucus* showed significant difference in age structure between the seasons ($\chi^2 = 21.37$, df = 4, $p < 0.001$), with the dry season contributing the lowest count ($n = 51$) of adults but the highest counts for sub-adults ($n = 16$) and juvenile ($n = 1$).

3.4 Reproductive state of the small mammals

When considered for each of the three most abundant species (*M. erythroleucus*, *M. minutoides* and *A. niloticus*),

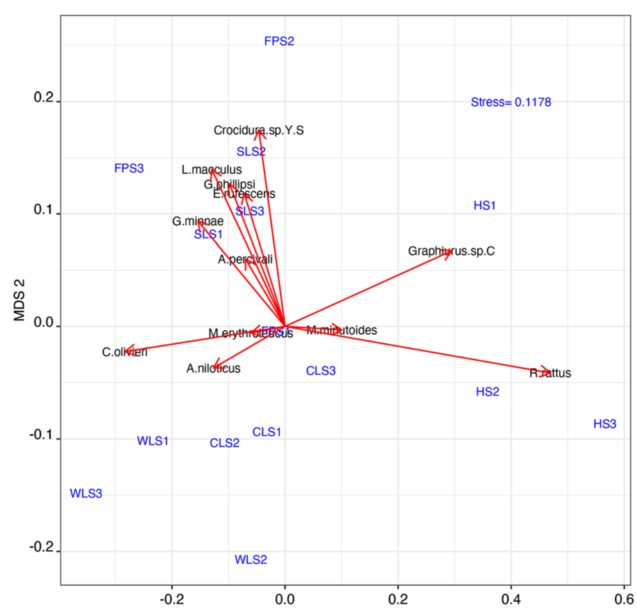

Figure 2: Non-metric multi-dimensional scaling (NMDS) plot depicting the composition of small mammals in the different spatio-temporal settings: cropland (CL), seasons (S1 = rainy, S2 = off-rain, S3 = dry). Similar habitat-season combinations apply to the forest patch (FP); scrubland (SL); wetland (WL) and homestead (H). The location of each species in the ordination space represents the spatio-temporal parameter to which it is associated. The lengths of arrows increase with increased strength of correlation between a small mammal species and a spatio-temporal parameter. The closer the distance between a pair of spatio-temporal parameters the higher their similarity in small mammal composition. The closer the distance between a pair of small mammal species the higher the likelihood for their co-occurrence.

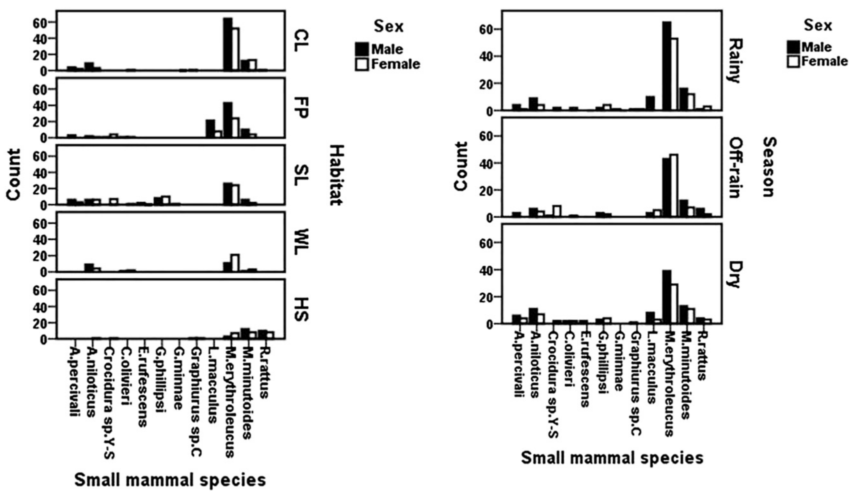

Figure 3: Sex structure of the small mammals according to the habitat types (CL = cropland; FP = forest patch, SL = scrubland; WL = wetland; HS = homestead) and seasons.

the reproductive activity of *M. erythroleucus* varied significantly ($\chi^2 = 14.24$, df = 6, $p < 0.05$) and barely significantly ($\chi^2 = 20.46$, df = 12, $p = 0.059$) between the seasons and the habitat types, respectively (Figure 5). *M. erythroleucus* scored the highest number ($n = 57$) of reproductive males in the rainy season followed by the off-rain ($n = 36$) and dry season ($n = 26$). The number of reproductive female individuals of *M. erythroleucus* was the highest for off-rain season ($n = 37$) followed by the rainy ($n = 32$) and dry ($n = 19$) seasons. Likewise, cropland contributed the highest number ($n = 48$) of reproductive male individuals of *M. erythroleucus* followed by the forest patch ($n = 38$), scrubland ($n = 20$) wetland ($n = 10$) and homestead ($n = 3$). Moreover, the number of reproductive female individuals *M. erythroleucus* was the highest in the cropland ($n = 40$) followed by the scrubland ($n = 16$), forest patch ($n = 14$), wetland ($n = 12$) and homestead ($n = 6$).

4 Discussion

This study reports nine species of rodents and three species of insectivorous small mammals: two species (*Crocidura* sp. and *C. olivieri*) belong to order Eulipotyphla and one species (*E. rufescens*) belongs to order Macroscelidea from a mosaic agricultural landscape adjacent to the western shore of Lake Abaya, Ethiopia. The overall small mammal species richness is higher in the current study compared to that reported by Demeke et al. (2007). This might be attributed among others to the underlining difference in the habitats and seasons surveyed. While our study reports a dozen small mammal species from an agricultural landscape, three of the small mammal species namely; *G. minnae*, *E. rufescens* and *Graphiurus* sp. "C" were very rarely encountered, with ≤ three individuals in the whole study period. The low numbers of the arboreal species, *G. minnae* and *Graphiurus* sp. "C" can

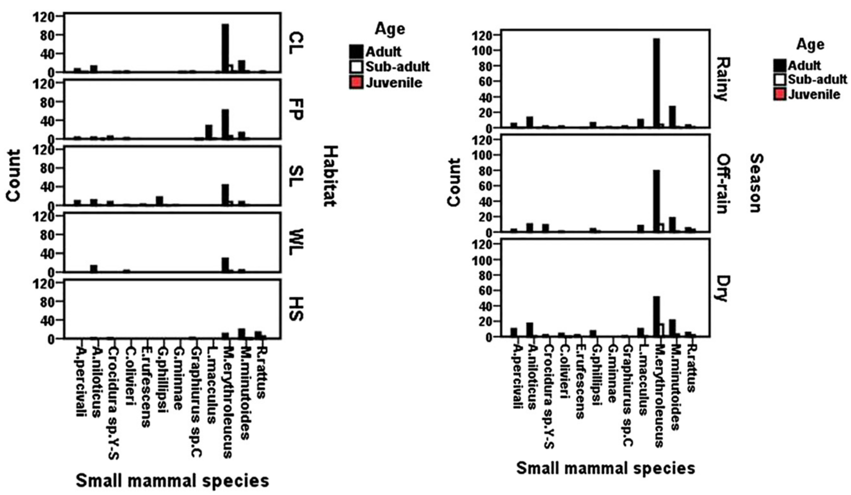

Figure 4: Age structure of the small mammals according to the habitat types (CL = cropland; FP = forest patch, SL = scrubland; WL = wetland; HS = homestead) and seasons.

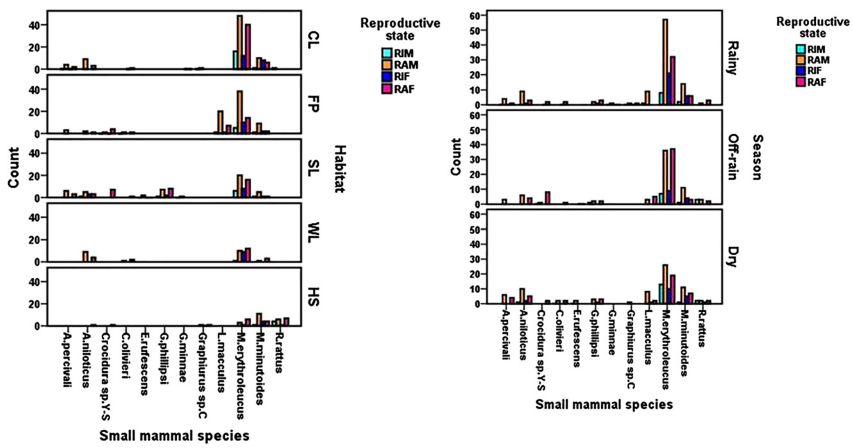

Figure 5: Reproductive activity of the small mammals according to the habitat types (CL = cropland, FP = forest patch; SL = scrubland; WL = wetland; HS = homestead) and season. RIM = reproductively inactive male; RAM = reproductively active male; RIF = reproductively inactive female and RAF = reproductively active female.

be ascribed to our trapping method that targeted ground dwelling small rodents.

As expected, diversity of the small mammals was lowest in the cropland compared to the non-crop habitats (including homestead). The results are in agreement with Demeke et al. (2007), Mayamba et al. (2019) and Shilereyo et al. (2019) who also reported higher small mammal diversities in non-cultivated areas than in agricultural fields in Ethiopia (Arba Minch area), Uganda and Tanzania, respectively. The low small mammal species diversity in cropland can be ascribed to higher disturbance due to human activities including; land preparation (ploughing), weeding, thinning of young plants (particularly maize) and harvesting.

M. erythroleucus was the most common species across the different habitats regardless of the year and seasons of sampling. The cropland scored the highest abundance of rodents dominated by *M. erythroleucus,* particularly during the rainy season. This finding is in agreement with Fichet-Calvet et al. (2009) who reported higher abundance of *M. erythroleucus* in cultivated areas during the rainy season in coastal Guinea, West Africa. Afework and Leirs (1997) and Workneh et al. (2004) also reported the dominance of *M. erythroleucus* in agro-ecosystems of central and northern Ethiopia, respectively. The dominance of *M. erythroleucus* in the human-modified habitats might be ascribed to its tolerance for wide ranging environmental conditions (Ba et al. 2012). In the current study, the higher proportions of *M. erythroleucus* and *A. niloticus* in year two might be linked to protracted rainfall in the area which was unusual and might have resulted in extended seasonal breeding, higher litter sizes and consequent population increase (Afework and Leirs 1997; Delany and Monro 1986).

Only few of *M. erythroleucus* were caught in homesteads. This might be attributed to avoidance of homesteads by this species due to the presence of *Rattus rattus*. It could also be that *M. erythroleucus* was outcompeted or repelled by *R.rattus*. These statements are supported by Monadjem et al. (2011) who also reported that the larger *R. rattus* repels *Mastomys* sp. from entering houses in smallholder systems of Africa. Poor housing structure, presence of live-fencings, improper handling of mango and banana wastage at harvest, as well as practice of using non-rodent-proof bags to store shelled maize indoors (Zewdneh et al. 2020) might have contributed to the preference of *R. rattus* for the homesteads. This is in agreement with Panti-May et al. (2012) and Alembrhan and Chelmala (2019) who also reported *R. rattus* to prefer impoverished rural homesteads.

M. minutoides was the second most abundant species across the different habitats despite its numerical dominance in the cropland. Earlier surveys also indicated the occurrence of *M. minutoides* in savannahs, forests, agricultural areas and rural homesteads (Bryja et al. 2014; Lamb et al. 2014). Recent genetic analysis by Bryja et al. (2014) also confirmed the ocurrence of the species in our study area. Though numerically the second most abundant in cropland and homestead habitats, *M. minutoides* is not recognized as a major agricultural pest in Africa (Mulungu 2017).

A. niloticus was the third most common species across the different habitats, with its occurrence in our study area matching the distribution of previously genotyped individuals from the ACB particularly, the Nech Sar National Park and human modified habitats at the eastern shore of Lake Chamo and northern shore of Lake Abaya (Bryja et al. 2019a). The association of *A. niloticus* with the wetland during the dry season and the likelihood of its occurrence in the cropland during the rainy season suggest possible movements of this species between the cropped and non-cropped areas in search of better food and cover in the different seasons (Delany and Monro 1985). For instance, during the rainy season, the dense hedgerow undergrowth at cropland margins and young maize plants can provide better cover and food, respectively to *A. niloticus* which is also diurnal in its foraging activity and may seek more cover against potential predators (Delany and Monro 1985).

A. percivali showed strong association with the scrubland during the dry season. The association of *A. percivali* with the dry conditions in the scrubland matches with its habitat requirements in the Afro-Arabia region (Aghová et al. 2019). The association of *A. percivali* with the cropland during the rainy season could suggest that the species could be a potential crop pest. However, there is no available evidence to suggest that *A. percivali* is a crop pest elsewhere in Africa (Mulungu 2017).

G. phillipsi was exclusively a scrubland species regardless of the year and season of sampling. The scrubland is part of the Saint Mary's churchyard and is drier (no incidence of being flooded) as it is located in an artificially raised area. According to ecological description of vegetation type, it is categorized under Acacia woodland (Mengesha et al. 2020) interspersed with thickets of shrubs mainly *A. fruticosa* (Yonas et al. 2020) and a seasonal herb (*Plectranthus marrubatus*), typical of the gerbil habitat in the Somali-Masai Savanna ecosystem (Aghová et al. 2017). However, the habitat is under progressive pressure as a result of cemetery expansion and intensive browsing by goats. The ongoing habitat loss may cause local extinction or dispersal of *G. phillipsi* to the nearby croplands where they may become serious pets. Gerbils are recognized as important pests of maize and root crops in Africa (Mulungu 2017).

L. macculus was limited to the forest patch regardless of the year and season of sampling and co-occurred with *C. olivieri* in the dry season. However, this habitat is vanishing due to ongoing overgrazing and trampling by cattle, charcoal making and collection of wood for fire or house construction. Moreover, during the rainy season, the habitat is inundated with massive runoff from the upland system and gets covered with sediment-displaced water from Lake Abya. These anthropogenic pressures are more likely to cause local extinction of *L. macculus* which generally inhabits high-grass savanna (Bryja et al. 2019b). Evidence also suggests that small mammal communities adapted to forest habitats are more likely to disappear in their natural habitats rather than crossing the forest-agriculture edge and dispersing into agricultural areas (Chapman et al. 2019).

Moreover, we captured transient small mammal species, namely; *G. minnae* (reported earlier from Arba Minch area) (Yalden and Largen 1992) and *E. rufescens* (reported earlier from bushland habitat in the Nech Sar National Park) (Sintayehu et al. 2011) from the scrubland and *Graphiurus* sp. "C" (reported to inhabit forests and woodlands of south-western Ethiopia) (Bryja et al. 2019b) from homestead and cropland in the study area. The occurrence of these species in the human-dominated landscapes means that they are also exposed to anthropogenic pressures and potential extinction locally. The arboreal species, *Graphiurus* sp. "C" and *G. minnae* (the latter is also endemic to Ethiopia and under vulnerable IUCN threat category (Lavrenchenko and Afework 2017)) seem to be associated with mango and forest remnant trees in the homestead and scrubland, respectively. However, this needs to be established with further surveying.

The age–sex structure of the rodents (except for *G. phillipsi*) was adult-male-biased. This might be due to the larger range size of adult males to find receptive females for mating according to the "female in space" hypothesis (Ostfeld 1990). But, it could also be that adult males moving across habitats might be repelled by territorial males defending spatially clustered females which might have also caused males' increased probability of being captured (Ostfeld 1990; Wolff 2007). However, we were unable to find evidence to support whether such territoriality exists among male individuals of the small mammal species investigated in this study to defend spatially clumped females. Nevertheless, earlier ecological surveys showed adult-male biased dispersals in *M. erythroleucus* (Odhiambo et al. 2005; Workneh et al. 2006) and *A. niloticus* (Delany and Monro 1985) in African smallholder agricultural systems.

M. erythroleucus has shown a clearly seasonal reproductive activity, occurring during the rainy (October) and off-rain (December) seasons, particularly in the cropland. The reproductive activity of *M. erythroleucus* in the cropland during the wet seasons might be associated with the quality food available during the August to December cropping season. This is in agreement with Leirs et al. (1994) and Flrouet et al. (1996) who established that germinating (young maize plants) can initiate sexual maturation in *Mastomys* species. Recently, Mlyashimbi et al. (2018) also reported the wet season to contribute higher proportion of vegetative food materials in the diet of *Mastomys natalensis* that also enhanced reproductive activity in this species.

5 Conclusion

This study demonstrated the abundance, diversity, spatiotemporal association and reproductive state of small mammals in the lowland agricultural systems adjacent to Lake Abaya, Ethiopia. *M. erythroleucus* was found to be a generalist species, abundantly occurring in multiple habitats irrespective of season. The large majority of seasonally reproducing male and female individuals also belonged to

M. erythroleucus and occurred in the cropland, signifying its agricultural pest importance. The likelihood of co-occurrence of *M. erythroleucus* with *A. niloticus* in the cropland during the rainy (maize planting) season and possible overlap in their preference to feed on young maize plants may suggest potentially high damage to the crops. Species limited to the scrubland (*E. rufescens* and *G. phillipsi*) and forest patch (*L. macculus*) are more likely to suffer local extinction due to ongoing destruction of their habitats. Though disconnected from protected area and under severe anthropogenic pressure, habitats such as the scrubland in the ACB can harbor diverse small mammal species including the rarely encountered ones such as *G. minnae* (which is also endemic to Ethiopia and under vulnerable IUCN threat category), *E. rufescens* and *Graphiurus* sp. "C". These results suggest the importance of anthropogenic habitats for ecosystem functioning and hence, should not be ruled out from conservation actions.

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Compliance with ethical standards: Small mammal trapping and sample collection were conducted with permission from the Arba Minch University and Gamo Zone Bureau of Environment, Forest and Climate Change Control. Verbal consent was obtained from the homestead and cropland owners prior to setting traps. A sample export permit (EBI 71/127/2019) was obtained from the Ethiopian Biodiversity Institute following the Nagoya Protocol for genotyping studies.

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