Afromontane mosaic vegetation acts as a barrier between small mammals from two savannah biomes in northern Ethiopia

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Abstract

Despite its biogeographical uniqueness, where two vast savanna regions are separated by the Afromontane mosaic vegetation, there is a significant lack of small mammal sampling in the Tigray region of Ethiopia. Leveraging all our available data on rodents and shrews in the region, we tested the hypothesis that the Afromontane mosaic vegetation in the highlands acts as a barrier to gene flow between taxa found in the Somali-Masai and Sudanian savanna in the southeast and western lowland parts of the region, respectively. Morphological and DNA sequence analysis confirmed the presence of 23 species of small rodents and shrews in the region. We recorded 18 of these species in the Afromontane mosaic vegetation, seven species in the Sudanian savanna, and four species in the Somali-Masai savanna. Notably, the fauna of Sudanian savanna was strikingly different from that of the Somali-Masai savanna at both intraspecific and interspecific level, suggesting northern Ethiopian highlands as very strong biogeographic barrier for taxa adapted to arid lowlands. However, the reported species diversity remains provisional, and additional sampling from unexplored areas is needed. Furthermore, some of the reported taxa, in this study, such as *Mus* cf. *tenellus*, *Crocidura* cf. *fuscomurina*, *Dendromus* sp. indet. 2, and *Otomys* cf. *cheesmani*, require detailed taxonomic investigation and may represent new species. A robust understanding of the taxonomic diversity and distribution of the small mammals in the region is crucial for effective conservation planning as well as for addressing practical questions related to rodents, such as in public health and pest management.

Introduction

Ethiopia hosts the Eastern Afromontane and Horn of Africa biodiversity hotspots (Mittermeier et al. 2004). It is the center of the East African region, which has eleven Afrotropical ecoregions and has been designated a Global 200, an ecoregion of global importance for biodiversity conservation (Olson and Dinerstein 2002). The country comprises diverse vegetation types, including the tropical lowland rainforest in the southwest, arid and semi-arid dry woodlands in the east, and Afroalpine forests in the north and southeast. Thus, the highest biodiversity in Africa both in flora and fauna is strongly associated with the geomorphological history of the region.

Based on Lillesø et al. (2011), the major potential natural vegetation types in the Tigray Region, northern Ethiopia, can be described in to five categories (Fig. 1);(i) Afromontane mosaic vegetation: which dominates the eastern escarpments of Hugumbrda-Grakahsu and Dese'a Forests. It covers a larger area in the region. It exhibits moderately gentle to steep scarps. It forms a climatic buffer zone between the highlands of the Tigray Region and the lowlands Tigray and the Afar Region by extending in an easterly direction along and down the northeastern escarpment; (ii) Afroalpine vegetation: these are located in the top mountains of Tsbet and Hugumbrda-Grakahsu forest; (iii) Ericaceous belt habitats, both limited to the patchy vegetation of the highest mountains in the region (e.g. Mount Tsbet); (iv) Somali-Masai savanna vegetation, limited to the *Acacia* (= Vachellia)-Commiphora deciduous bushland and thickets from the border of the Afar Region; and (v) Sudanian savanna vegetation, covering most of the western and northwest part of the region, including the Kafata-Humera and Kafta-Sheraro National Park; The eastern highland escarpments (the end of the north-western escarpments of the Ethiopian Great Rift Valley) are the only remnant sites with fragmented Afromontane forest cover left in the region.

Despite its biogeographical uniqueness, where two vast savannas (Somali-Masai and Sudanian) are separated east-west by Afromontane mosaic vegetation, there is a significant lack of sampling of small mammals in Tigray to investigate the role of the Afromontane mosaic vegetation as a barrier for gene flow (see the sampling gap in Bryja et al. 2019a). In comparison, available data for Tigray are biased towards the Afromontaine mosaic region, crop fields, and, to some extent, peri-domestic areas (Adam et al. 2015; Kiros et al. 2020; Meheretu et al. 2012, 2013, 2014,). Though still limited in intensity, the current sampling has covered samples from the five vegetation types that can provide valuable information through integrative taxonomic and biogeographical analyses.

This paper summarizes all available data on the diversity of small mammals in Tigray, based on both our past and recent collections. It also presents the first comprehensive information about the distribution and taxonomic status of the species in the region, using georeferenced genetic data obtained from mitochondrial DNA markers to assess their evolutionary relationships. Our aim was to test the hypothesis that the Afromontane mosaic vegetation serves as a barrier to gene flow between taxa found in the Somali-Masai and Sudanian savannas. Although we could not document the entire rodents and shrews of the entire region (e.g. sampling is missing from the northeast and southwest of the region), this study represents the first of its kind for the region and marks the initiation of systematic documentation of the small mammals from the major vegetation types of Tigray.

Materials And Methods

Description of the study areas

Small mammal sampling was conducted in the five major potential natural vegetation areas of nine sampling locations in Tigray: namely, the Kafta-Sheraro National Park (KSNP), Mai-Temen, Hagereselam, Agula'e, Atsbi, Mekelle, Mount Tsbet, Hugumbrda-Grakahsu Forest, and the Raya Valley (see Table 1). Based on Lillesø et al. (2011); the specific localities represent the major (potential) natural vegetation types: Afromontane mosaic vegetation (e.g. Mekelle, Hagereselam, Agula'e, Atsbi, and Hugumbrda-Grakahsu Forest, and lower parts of Mount Tsbet), Afroalpine and Ericaceous belt (e.g. highest parts of Mount Tsbet, and Hugumbrda-Grakahsu forest), Somali-Masai savanna (the Raya valley of Alamata and Abergel fattening farm) and Sudanian savanna (e.g. KSNP, and Mai-Temen) (Fig. 1; Table 2).

Table 1

Description of the nine trapping localities: (1) Kafta Sheraro National Park (KSNP); (2) Mai-Temen; (3) Hagereselam; (4) Agula'e; (5) Atsbi; (6) Mekelle; (7) Tsbet; (8) Hugumbrda-Grakahsu forest; (9) Raya Valley. Names within brackets are specific trapping sites within localities.

Sampling localities	Habitat description	Altitude (m a.s.l)
KSNP (e.g. Endamekayie and Mentadubu'e)-	Traps were set in forests comprising broad-to-fine-leaved deciduous habitat (e.g. Mentadubu'e) and in the lower reaches of the wide Tekeze valley (e.g. Endamekayie) in a broken terrain dominated by *Acacia– Combretum* woodland with large trees of *Adansonia digitata* and *Tamarindus indica.*	500–600
Mai-Temen	On the higher eastern plateau of the KSNP, cultivated, wooded grassland thrives. Much of the area would naturally be covered in edaphic tall grassland, with some patches of woody species such as *Balanites aegyptiaca.*	1000
Hagereselam (e.g. Mahbereslassie)	Bushland on steep slopes and crop fields on lesser slopes with stone bunds are typical land uses in the Afromontane mosaic vegetation. The vegetation is largely dominated by *Rumex nervosus*, *Acacia ethbaica*, and *Eucleas himperi*.	2584
Agula'e (e.g. Kihen and Girambaro)	Traps were set at specific localities in Kihen: an "area enclosure" protected for many years for land rehabilitation in the region and characterized as bushland dominated by *Acacia ethbaica*, and at Girambaro in irrigated crop fields.	2000–2400
Atsbi (e.g. Dese'a forest and Golgol Na'ele)	Samples were collected in the Dese'a forest priority area, characterized as a dry evergreen forest dominated by *Juniperus procera*, and at Golgol Na'ele in rain-fed agricultural crop fields.	2000–2794
Mekelle (e.g. Mekelle University)	Samples were set in grass within a nursery site at the Endayesus campus of Mekelle University.	2018
Tsbet Mountain	Ericaceous belt and typical sub-Afroalpine vegetation composed of *Bidedn macroptera, Kniphofia foliosa, Festuca macropylla*, *Hypericum* sp., and *Helichrysum* sp.	3000–3965
Hugumbrda-Grakahsu forest	Both are categorized as dry evergreen montane forests, dominated by *Juniperus procera* at middle altitudes and mosaic vegetation and an ericaceous belt composed of *Erica arborea, Bidedn macroptera*, *Kniphofia foliosa*, and *Festuca macropylla* at higher altitudes.	1700–3000
Raya Valley (e.g. Alamata and Abergele fattening farm)	Samples were collected at specific localities in Alamata and at the Abergele fattening farm. Traps were set in both crop fields and fallow lands dominated by sparse *Acacia oerfota* and *Cadia purpurea* trees.	1400–1500

Table 2

List of rodents and shrews of the Tigray region, northern Ethiopia. Sampling localities are grouped into 9 geographical locations (see Fig. 1).The species was captured in that particular locality (√), and the species is not captured in that particular locality (-).

Taxon	KSNP (SS)	Mai-Temen (SS)	Hagereselam (AM)	Agula'e (Am)	Atsbi (Am)	Mekelle (Am)	Mount Tsbet (Am)	Hugumbrda-Grakahsu forest (Am)	Raya Valley (SMS)
(A) Species confirmed by trapping in this study									
Family Nesomyidae									
Dendromus sp. indet. 2 (sensu Voelker et al. in lit.)	-	-	-	-	-	√	-	-	-
Family Muridae									
Subfamily Murinae									
Arvicanthis niloticus (É. Geoffroy Saint Hilaire, 1803)	√	-	√	√	√	√	-	√	√
Arvicanthis raffertyi Frick, 1914	-	-	-	-	-	-	-	-	√
Desmomys harringtoni (Thomas, 1902)	-	-	-	-	-	-	√	√	-
Mus mahomet Rhoads, 1896	-	-	√	√	√	√	√	√	-
Mus cf. *tenellus* (sensu Bryja et al. 2014)	-	-	√	√	-	√	-	-	-
Mus proconodon Rhoads, 1896	-	-	-	√	-	-	-	-	-
Mastomys awashensis Lavrenchenko et al. 1998	√	√	√	√	√	√	-	√	√
Mastomys kollmannspergeri (Petter, 1957)	-	√	-	-	-	-	-	-	-
Ochromyscus brockmani (Thomas, 1906)	-	-	-	√	-	-	-	√	-
Otomys simiensis Taylor et al. 2011	-	-	-	-	-	-	√	-	-

According to Lilles et al. (2011), the nine sampling locations' abbreviations within brackets indicate the types of vegetation; Am = Afromontane mosaic; SMS = Somali-Masai Savanna and SS = Sudanian Savanna

Taxon	KSNP (SS)	Mai-Temen (SS)	Hagereselam (AM)	Agula'e (Am)	Atsbi (Am)	Mekelle (Am)	Mount Tsbet (Am)	Hugumbrda -Grakahsu forest (Am)	Raya Valley (SMS)
(A) Species confirmed by trapping in this study									
Family Nesomyidae									
*Otomys cf. cheesmani (*sensu Mizerovská et al. submitted)	-	-	-	-	-	-	-	√	-
Rattus rattus (Linnaeus, 1758)	-	-	√	√	√	√	-	-	√
Stenocephalemys albipes (Rüppel, 1842)	-	-	√	√	√	√	√	√	-
Subfamily Deomyinae									
Acomys cahirinus (É. Geoffroy Saint-Hilaire, 1803)	-	√	√	√	√	√	-	√	-
Acomys sp. "Cah7" (sensu Aghová et al. 2019)	√	√	-	-	-	-	-	-	-
Acomys sp. "Cah8" (sensu Aghová et al. 2019)	√	-	-	-	-	-	-	-	-
Acomys mullah Thomas, 1904	-	-	-	-	-	-	-	-	√
Lophuromys simensis Osgood, 1836	-	-	-	-	-	-	√	√	-
Subfamily Gerbillinae									
Gerbilliscus robustus (Cretzschmar, 1826)	√	-	-	-	-	√	-	√	√
Family Gliridae (dormice)									
Graphiurus sp. "B" (sensu Bryja et al. 2019)	-	-	√	-	-	-	-	√	-
Family Soricidae									
Crocidura olivieri Lesson, 1827	-	-	√	√	√	√	-	√	√
Crocidura cf. fuscomurina	-	-	-	√	-	-	-	-	-

According to Lilles et al. (2011), the nine sampling locations' abbreviations within brackets indicate the types of vegetation; Am = Afromontane mosaic; SMS = Somali-Masai Savanna and SS = Sudanian Savanna

Taxon	KSNP (SS)	Mai-Temen (SS)	Hagereselam (AM)	Agula'e (Am)	Atsbi (Am)	Mekelle (Am)	Mount Tsbet (Am)	Hugumbrda-Grakahsu forest (Am)	Raya Valley (SMS)
(A) Species confirmed by trapping in this study									
Family Nesomyidae									
(B) Reported from neighbouring regions									
Family Ctenodactylidae									
Pectinator spekei (Blyth, 1856), with in the range of Dese'a forest bordering the Afar region to the east (Wilson, 2019)									
Subfamily Deomyinae									
Acomys louisae (Thomas, 1896), occurs at low elevations in Afar at the border with Tigray									
According to Lilles et al. (2011), the nine sampling locations' abbreviations within brackets indicate the types of vegetation; Am = Afromontane mosaic; SMS = Somali-Masai Savanna and SS = Sudanian Savanna									

The majority of the area in the western and center parts of the region, respectively, is covered by the Sudanian savanna and the Afromontane mosaic vegetation. The eastern portions of the Raya Valley have the Somali-Masai savanna, and the middle Pick Mountains contain the Ericaceous belt and Afroalpine vegetation. Chain Mountains connect the Afromontane mosaic and Afroalpine vegetation habitat; with the highest point at Mount Tsbet (3955 m) above sea level (a.s.l.). The uppermost of these mesic highlands are dominated by species like *Erica arborea, Bidedn macroptera, Kniphofia foliosa*, and Guassa (*Festuca macropylla*). They are also proximate to the Afroalpine habitats of the Abohoy Gara and Semen Mountains. The eastern directions of the dry Afar lowlands with *Acacia* woodlands are located at a short distance (ca. 5–10 km) from these habitats. The Somali-Masai savanna vegetation, the eastern part of Tigray (e.g. Alamata and Abergele), is part of the northwestern end of the Ethiopian Great Rift Valley and shares many characteristics with the Afar region. The Sudanian savanna vegetation (e.g. KSNP and Mai-Temen) covers a vast area of western Tigray bordered by Sudan and Eritrea. The Afromontane mosaic vegetation separates these two savanna biomes (see Fig. 1).

The Afromontane mosaic vegetation comprises mainly two forest priority areas (Hugumbrda–Grakahsu and Dese'a forest) and is located along the Ethiopian Great Rift Valley's end of the north-western escarpment, particularly facing the Afar depression. The Hugumbrda–Grakahsu forests are an isolated forest not only because the surrounding area has been cleared but also because it is situated in a secluded valley next to the parallel rift of Lake Hashenge. Second is the Dese'a forest, of which a large part lies in the Tigray region and a smaller area in the Afar region. They are also both broadly categorized as "dry single-dominant Afromontane forests," which are characterized by a dry climate (annual precipitation less than 1000 mm) and with *Juniperus procera* in the canopy and *Olea europaea* as the dominant tree species (Friis 1992). They form dry, evergreen natural forest ecosystems where the climate is influenced by topography and exposure to rain-bearing winds (Nyssen et al. 2005). In the region, the wet rainfall season is between June and September, while the remaining months are more or less dry.

Collections Of Rodents And Shrews (Hereafter Small Mammals)

Small mammals were collected from 2012 to 2020 from the five potential vegetation types in nine different localities. We have also used data on small mammals from past collections by the authors at different times. Raya Valley and Hugumbrda-Grakahsu forests were sampled in November 2012, March 2017, and February 2020. The other districts, KSNP, Mai-Temen, Hagereselam, Agula'e, Atsbi, Mekelle, and Mount Tsbet, were sampled from 2019 to 2020. Small mammals were sampled using Sherman's live traps (23 × 9.5 × 8 cm). Traps were set on several diverse habitats within the major potential natural vegetation types to maximize species diversity.

To trap small mammals in the Hugumbrda-Grakahsu forest, one 60 x 60 m square grid, one in bushland, and another in grassland habitats were set up between November 2012 and March 2012. Each grid consisted of seven parallel lines, 10 m apart, with trapping stations (i.e. a total of 49 trapping stations per grid). Grids were later avoided due to unsuitable mountains and dense thorny bushlands. Then, line transects (LTs) were applied to sample all localities. Stanley et al. (2007) also described an efficient method in which trap lines caught most of the rodent species for the survey.

Each habitat had two line transects 50 m apart, with 50 trapping stations (each with 50 traps) spaced 2 m apart. All traps were baited with peanut butter mixed with barley flour and checked every morning. Traps were inspected for three consecutive days. Captured rodents and shrews were handled in accordance with the Guidelines of the American Society of Mammalogists for the use of wild animals in research (Gannon et al. 2007). Specimens were weighed and the body, tail length, ear length, and hind foot length were measured. Preliminary species identification, sex, reproductive condition, and other formative details were also noted at the time of capture. The animals and tissue samples from representative animals, including liver, kidney, spleen, and heart, were taken and preserved in ethanol (96%) for further molecular studies and kept in the Department of Biology, Mekelle University, Ethiopia. DNA barcoding was used to confirm the identification of representative small mammal species at the Institute of Vertebrate Biology, Czech Academy of Sciences, Czech Republic. We also presented some photos of the representative small mammals as supplementary material (see Supplementary 1). All fieldwork complied with legal regulations in Ethiopia, and sampling was undertaken with the permission of the Ethiopian Wildlife Conservation Authority (permission no. EWCA Ref. No. 31/248/2010).

Results And Discussion

Using morphological and DNA sequence analysis, we confirmed a total of 23 species of small mammals in Tigray (Table 2). The small mammals belonged to 14 genera from four families. Rodents were dominated by the family Muridae, with representatives of three subfamilies: Murinae by 13 species (which accounted for 57% of the total captures), Deomyinae by five species (22%) and Gerbillinae by one species (4%). Each of the families Nesomyidae and Gliridae were represented by one species (4%). Shrews (family Soricidae) belonged to two species (9%). Nine of the total species (40%) (*Dendromus* sp. indet. 2, *Desmomys harringtoni, Lophuromys simensis, Mastomys awashensis, Mus mahomet, Mus proconodon, Otomys simiensis, Stenocephalemys albipes,* and *Graphiurus* sp. "B") were endemic to Ethiopian Highlands (see Bryja et al. 2019a). Eighteen of the small mammal species were recorded in the Afromontane, Ericaceous belt and Afroalpine in Tigray, seven species in the Sudanian savanna, and four species in the Somali-Masai savanna (Table 2). Four species, *Mastomys kollmannspergeri*, *Acomys* sp. "Cah7" and *Acomys* sp. "Cah8" were restricted to the Sudanian savanna, while *Acomys mullah* to the Somali-Masai savanna. On the other hand, *Mastomys awashensis* was found in all vegetation types, but avoided higher altitudes (>3000m a.s.l.).

The northern region of Ethiopia, particularly the Tigray region, has experienced significant human-induced land use changes over the years. Some of the major drivers of these changes include population growth, agricultural expansion, deforestation, and climate change (Nyssen et al. 2008). Particularly the Afromontane mosaic vegetation has been severely affected by, agricultural expansion. We recorded 21 species of rodents and 2 shrew species in the region. Based on the overall number of rodents and shrews in Ethiopia (Bryja et al. 2019a; Lavrenchenko et al. 2009), this diversity corresponds to about 20% of rodent species and 8% of shrew species in Ethiopia. Even though it is difficult to compare the small mammals diversity of the Tigray region with the current species reported from the neighbouring Afar region (16 rodent species) (Bryja et al. 2022), especially due to differences in vegetation type and the approaches used for species delimitations, the diversity in the Tigray region seems much higher. Based on the patterns of distribution and ecological requirements, we can separate the recorded taxa into four groups that are specified in more details below.

Widespread species across vegetation types in Tigray

Mastomys awashensis (Lavrenchenko et al. 1998)

(Fig. 1 S1)

Previously, the species was thought to be endemic to the River Awash valley (Lavrenchenko et al. 1998). However, increasing genetic data suggests that the species may be more widespread in Ethiopia (Colangelo et al. 2010; Martynov et al. 2020; Bryja et al. 2022). During our sampling in Tigray, we recorded the species in eight sites within three major vegetation types (Somali-Masai savanna, Afromontane mosaic, and Sudanian savanna) (see for complete map in Bryja et al. 2022). It was abundant in all of the localities sampled (Table 2), but avoided high elevations. It coexists with *A. niloticus* and *S. albipes* in a broader range of habitats, including pre-domestic area, crop fields, fallow lands, and bushlands. *Mastomys awashensis*wassympatric with *M. kollmannspergeri* in the Sudanian savanna vegetation, particularly at Mai-Temen (Martynov et al. 2020). The species is known as a serious agricultural pest in Tigray (Kiros et al. 2020; Meheretu et al. 2014).

The African grass rat (*Arvicanthis niloticus* É. Geoffrey, 1803)

(Fig. 2 S1)

In Tigray, we discovered two genetically distinct populations of *A. niloticus* s. str. (sensu Bryja et al. 2019; = C1 clade in Dobigny et al. 2013) separated by the Afromontane mosaic vegetation. The first subclade (red circle) occurring in Somali-Masai savanna and Afromontane mosaic vegetation (e.g. Raya Valley, Hugumbrda-Grakahsu forest, Mekelle, Agula'e, Atsbi, and Hagereselam), and the second subclade (green circle) occurring in Sudanian savanna vegetation (e.g. KSNP) to the west (Fig. 2). While the first subclade is similar to the subclades of *A. niloticus* s. str. recorded from Lake Tana and Alatish National Park, the second subclade is similar to the Rift Valley subclades (see Bryja et al. 2019b). Another species, *A. rafferty*iwas known from the Somali-Masai savanna of the region, particularly from the escarpment in the Alamata area (Bryja et al. 2019b; Bryja et al. 2022), which is sympatric with *A. niloticus (the* first subclade*) but allopatric with the second subclade living in the* Sudanian savanna vegetation of the western part of Tigray. Based on our collection, *Arvicanthis niloticus (*the first subclade)was **recorded** in six sites across the region, from the eastern to the central highlands. During our collection, it was also common in crop fields, irrigated fields, fallow lands, grasslands, and bushlands, with an elevation range of 1500–2871 m a.s.l. It is a serious agricultural pest particularly in crop fields in the region (Kiros et al. 2020; Meheretu et al. 2014).

Spiny mouse (*Acomys* I. Geoffroy, 1838)

(Fig. 3 S1)

Based on genetic data, we identified four spiny mouse species for Tigray: *Acomys mullah*, *A.* spp. A (Lavrenchenko et al. 2011; = Cah 8 in Aghová et al. 2019), *A* spp. B (Lavrenchenko et al. 2011; = Cah 7 in Aghová et al. 2019), and *Acomys cahirinus* (É. Geoffroy Saint-Hilaire, 1803; = Cah 10 in Aghová et al. 2019) (see Fig. 3). Note that the taxonomic statuses of the three spiny mice (*A.* spp. A, *A.* spp. B, and Cah10) should be further researched. They differ in karyotype (Lavrenchenko et al. 2011) and physiological and behavioral traits (Ivlev et al. 2011). *Acomys* spp. A and *A.* spp. B, are sympatric in the Sudanian savanna vegetation. *Acomys* spp. B and *A. cahirinus* have contact zones in thewestern Sudanian savanna vegetation. However, *Acomys mullah* from the Somali-Masai savanna is separated from the other three species by Afrotropical mosaic vegetation. An additional species, *Acomys louisae,* which is an endemic to Afar but will occurs at low elevations in the Tigray in areas bordering Afar, and it may be sympatric with *A. mullah. Acomys cahirinus* was found in six locations, but *Acomys mullah* was only recorded in the Alamata region of the Raya Valley.

Species of the Ethiopian Highland endemics recorded in Tigray

White-footed Ethiopian Rat *Stenocephalemys albipes* (Rüppel, 1842)

(Fig. 4 S1)

Stenocephalemys albipes was recorded with an altitudinal range of 1500–3820 m above sea level, it was caught at most Afrotropical trapping sites (Fig. 4), with the exception of the drier parts of the western and eastern Tigray Savannas. The species occurs in variety of habitats, including pre-domestic, crop fields, bushlands, montane forest, and the Afroalpine Erica scrub (Kiros et al. 2020; Mizerovská et al. 2020; Bryja et al. 2018a; Meheretu et al. 2012, 2013). In our collection, *Stenocephalemys albipes* was collected from six sampling localities. Particularly in Hagereselam, it accounted for 31% of the rodents sampled from pre-domestic areas. In Mount Tsbet too, the species accounted for 31% of total the rodents sampled, placed second only to the abundant species, *L. simensis*.

Harrington's rat *(Desmomys harringtoni* Thomas, 1902)

*D. harringtoni*was sampled only from Mount Tsbet and Hugumbrda-Grakahsu forest in Southern Tigray (2000-3820 m a.s.l.). In Hugumbrda-Grakahsu forest, it was sampled from moist woodland and Erica scrub, including Embasadeg, Wenbert, and Menkere. Bryja et al (2019a) reported the species from several localities in the Ethiopian Highlands, on both sides of the Rift Valley. The population from Tigray genetically belongs to the northern clade of the species (sensu Kostin et al. 2020).

Mahomet mouse *(Mus mahomet* Rhoads, 1896)

(Fig. 5 S1)

The species was captured at six sites during our study period (Table 2), most frequently from the Afrotropical mosaic habitat of the area with an altitudinal range (1700-3800m a.s.l.). It was associated with dense grasses and bushes. Additionally, the species was discovered in the *Bidedn macroptera* dominated Afroalpine ecosystem of Mount Tsbet (3820 m a.s.l.) (Fig 4). The species' altitudinal range, according to Yalden (1988), is 1500–3200 m above sea level.

African Dormouse *Graphiurus* sp. B

(Fig. 6 S1)

Two Graphiurus spp. B, were captured in Hugumbrda-Grakahsu forest near Alamata and Hagereselam, separated by 230 km (Fig. 4). In Hugumbrda-Grakahsu forest, the individual was captured in *Opuntia ficus-indica* and *Acacia* spp. dominant bushland habitat at an altitude of 1500 m a.s.l. while in Hagereselam, the other individuals was captured in a pre-domestic area near stone bunds at an altitude of 2582 m a.s.l. According to Bryja et al. (2019a), the species has a wide distribution across the Ethiopian Highlands on both sides of the Rift Valley with an altitudinal range of 1945–3200 m a.s.l.

Otomys simiensis (Taylor et al. 2011) and *Otomys* cf. *cheesmani* (sensu Mizerovská et al., submitted)

(Fig. 7 S1)

The species was originally described as an endemic of the Semien Mountains (Taylor et al. 2011), but a wider distribution was suggested by Bryja et al. (2019a). However, recent genomic and morphometric analysis (Mizerovská et al. submitted) provides evidence that, *O. simiensis* is actually a narrowly endemic species found only of in the highest mountains of northern Ethiopia, e.g. Semien Mountains and Abohoy Gara. In Tigray, it was genetically confirmed only from Mount Tsbet where it was captured in a habitat vegetated with *Bidedn macroptera* and *Kniphofia foliosa* at an altitude of 3820 m a.s.l.

The individuals collected from Hugumbrda-Grakahsu forest with an altitudinal range of 2000 –3500 m a.s.l were genetically confirmed as *Otomys* cf. *cheesmani* (sensu Mizerovská et al. submitted) and possibly represent a new, yet undescribed species. Hugumbrda-Grakahsu forest is very close to Mount Tsbet (approximately 30 km) and is connected it by an undulating chain of mountains. Comparing their habitat, *Otomys* cf. *cheesmani,* seems to occupy the Afromontane mosaic habitat dominated by *Juniperus procera* and up to the ericaceous belt, while *O. simiensis* occupies a typical Afroalpine habitat, similar to the Semien Mountains, where it was first described by Taylor et al. (2011). The two species

thus seem to occupy separate altitudinal ranges, where *O.* cf. *cheesmani* in lower elevations as it was also found in wet grasslands close to Kombolcha at 2600 m a.s.l.; Bryja et al. 2019a, Mizerovská et al. submitted).

Ethiopian brush-furred rat*Lophuromys simensis* (Osgood, 1836)

In Tigray, Hugumbrda-Grakahsu forest and Mount Tsbet, with an altitudinal range of 2404–3657 m a.s.l., were the two locations where *Lophuromys simensis* was caught. However, the species seems more abundant at the lower altitudes of humid forests and sub-Afroalpine in the highlands, which is in agreement with previous reports (Kostin et al. 2019; Bryja et al. 2019; Komarova et al. 2021).

(Semi-) commensal/invasive speciesin Tigray

African giant shrew*, Crocidura olivieri* (sensu Jacquet et al. 2015)

Crocidura olivieri was captured from three sites: Hagereselam, Aagula'e, and Atsbi. Although it also occurred in crop fields, bushlands, and montane evergreen forests with an elevational range of 2200–2794 m a.s.l., it was particularly common in pre-domestic areas of Hagereselam and Atsbi. The species has also been reported in crop fields in Hagereselam with a preference for high stone bund density (Meheretu et al. 2014). The species is a widely distributed across Africa, from Senegal in the western to Ethiopia in the eastern, can be found well-vegetated moist habitats, such as lowlands and montane evergreen forests (Jacquet et al. 2015; Lavrenchenko et al. 2016).

Black rat *Rattus rattus* (Linnaeus, 1758)

Mus musculus and *Rattus rattus* are the only commensal rodents that have been introduced in Ethiopia (Bryja et al. 2019a), but only *R. rattus* was recorded in this study. We captured the species in domestic and pre-domestic areas of Hagereselam, as well as in irrigated crop fields in Aagula'e, which were located away from human settlements. The altitude range of these area was 2200-2584 m a.s.l. In contrast, Bryja et al. (2019a) reported capturing the species at higher elevation (3270m a.s.l.) in a house located in the Borena Saynt National Park.

Taxa with poor taxonomic/distributional knowledge in Tigray

The fringe-tailed gerbil *Gerbilliscus robustus* (Cretzschmar, 1826)

(Fig. 8 S1)

Two genetically distinct populations of *G. robustus* were found in Tigray (see Fig. 6): The first one referred to as R1 in Aghová et al. (2017), was found in the Raya Valley, Hugumbrda-Grakahsu forest and Abergele fattening farm. The second genetic clade, referred to as R2 in Aghová et al. (2017) inhabits western Tigray in Sudanian savanna vegetation (e.g. KSNP), indicating that the two populations are parapatric with a possible contact zone in the northern part. Genetic differences between the two clades are very high (see Bryja et al. 2022) and further research in the contact zone is necessary to determine whether they can hybridize or not (i.e. whether they represent two distinct biological species).

Delicate Pygmy Mouse, *Mus* cf. *tenellus* (Thomas, 1903)

This lineage of the delicate pygmy mouse was previously reported from two close localities in Tigray, Hagereselam and Mekelle (Bryja et al. 2019a; Bryja et al. 2014). During this study, two individuals were caught in the same trap line on the border of an irrigated crop field close to the Agula'e River, situated to the north of Mekelle and east of Hagereselam. The habitat of the captured individuals could be described as a grassland with an altitudinal range of 2000–2794 m a.s.l. dominant by *Acacia* spp. trees. Though it is likely that the species is endemic or nearly endemic to the Tigrayan highlands, more sampling efforts and genetic research are needed to unequivocally determine its taxonomic status, as well as characterize its distribution and ecological needs.

Mus proconodon (Rhoads, 1896)

In this study, *Mus proconodon* was genetically confirmed from a single individual sampled from Aagula'e. The individuals was found in high grass of *Hyparrhenia hirta* near *Acacia ethbaica* tree*,* at an elevation of 2200 m a.s.l. The species is considered a valid endemic species to Ethiopia (Yalden et al. 1976) and is one of only a few endemic Ethiopian mammals living in savanna-like habitats (Bryja et al. 2014; Lavrenchenko and Bekele 2017). Musser and Carleton (2005) had previously synonymized this species with *M. setulosus,* but Bryja et al. (2014) described that genetically, it represents the most distinct lineage in the whole the *setulosus*clade, clearly setting it apart from the true *M. setulosus* found in western Africa.

White-bellied Rocky mouse *Ochromyscus brockmani* (Thomas, 1908)

This species was captured at two different sites about 220 km apart: Hugumbrda-Grakahsu forest near Alamata and Girambaro near Agula'e, with an altitudinal range of 1700-2000 m a.s.l. In Hugumbrda-Grakahsu forest, it was captured in bushland dominated by *Acacia* spp., while in Girambaro, it was captured at the edge of an irrigated crop field with high herbaceous along the Agula'e River. Following the recent taxonomic revision of the tribe Praomyini by Nicolas et al. (2021), the previous generic name *Myomyscus* was changed to *Ochromyscus*. As part of this revision, Nicolas et al. (2021) proposed the English name White-bellied Rocky Mouse to *Ochromyscus*, because of the typical purely white belly all the species belonging to the genus possess and most preferred habitat of rocky outcrops, where they are known to abundantly occur. Using additional genetic and morphological data, Meheretu et al. (submitted) reported that *O. brockmani* was distributed in a part of the Afar Triangle, eastern Ethiopia, and Somaliland (see also Bryja et al. 2019a).

Crocidura cf. *fuscomurina*

Two individuals of *Crocidura* cf. *fuscomurina* were sampled from Agula'e at an altitude of 2200 m a.s.l in bushland dominated by *Acacia etbaica*, and genetically confirmed. This could be the first record of *C.* cf. *fuscomurina* in Ethiopia, particularly from this semi-arid region, signifying the presence of additional cryptic species that require further sampling and investigation using integrative taxonomy.

African climbing mice, *Dendromus* sp. indet. 2 (sensu Voelker et al., in lit.)

Two individuals of the *Dendromus* sp. indet. 2 were sampled from the Endayesus campus of Mekelle University at elevation of 2018 m a.s.l., among the grasses on the University nursery site. The only other species of the genus known to exist in the highlands of Tigray is *Dendromus mystacalis* found close to Axum (14.08 N, 38.45 E) (Dieterlen 2009). Although the mtDNA sequences of the two individuals are different from that of *D. mystacalis*, they are very similar to a single specimen of the genus collected in the Borena Saynt NP in central Ethiopia (Mulualem et al. in prep.). However, further sampling and integrative analysis is necessary to resolve the taxonomy of African climbing mice.

Pectinator spekei (Blyth, 1856)

The species was not recorded during our collection. The new location by Wilson (2019) for *Pectinator spekei* in the Afar region indicated that it is within the range of the Dese'a forest in Tigray at the border with the Afar region. The Dese'a forest, of which a large part lies in the Tigray region and a smaller area in the Afar region. On January, 2020, we have seen the species about 1km from Berahle (13.53 N, 40. 05 E) on the way to Hamed Ela moving near the entrance to a rock burrow (Per. Obs.)".

Conclusion

In this study, we used both our past and present collections to compile all the information on the rodent (n = 21) and shrew (n = 2) species found in the Tigray region, across different vegetation types. However, the Afrotropical mosaic vegetation

type was intensively sampled as part of a larger project focusing on the Afrotropical and Afroalpine regions, resulting in in higher species diversity in this vegetation type. Our findings clearly indicate that, the fauna of Sudanian savanna are strikingly different from that of the Somali-Masai savanna, both at intraspecific and interspecific levels, indicating that the northern Ethiopian highlands act as a very strong biogeographic barrier for taxa adapted to arid lowlands.

Our sampling intensity was clearly biased towards the Afromontane mosaic regions and crop fields in the eastern and southern parts of the region. Thus, data from the western Sudanian savannah vegetation (e.g. Kafta Humera, Dansha), some other Afrotropical mosaic vegetation (e.g. the highlands of Tselemti and Tsegedie), and the eastern part of the Somali-Masai vegetation (e.g. parts bordering Tigray and Afar), remain largely missing, hence requiring intensive surveys to fill these gaps. Similarly, the northern most highlands of the region, including parts of the Afrotropical mosaic vegetation of the chain of mountains around Adigrat and Erob that border with Eritrea are still largely unexplored.

Overall, the small mammals species diversity of the Tigray region is certainly provisional, awaiting additional sampling from the areas unexplored and detailed taxonomic revisions to resolve the specific status of some enigmatic taxa. For instance, specimens such as *Mus* cf. *tenellus, Crocidura* cf. *fuscomurina, Dendromus* sp. indet. 2 and *Otomys* cf. *cheesmani* sampled from the Afrotropical mosaic vegetation and as well as those sampled from the Sudanian savanna and Somali-Masai biomes may indicate, the presence of new species. Documenting the taxonomic diversity and distribution of the small mammals of the region provides valuable information that can be used to help planning future research questions and conservation efforts.

Declarations

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Contributions

KW, YM, JB, RHM conceptualized the study; KW, GM, FK, WH collected the samples; KW analysed the data; JB, GM analysed genetic data and produced the maps; KW wrote the first version of the manuscript; YM, JB reviewed it. All authors read, revised, and approved the final manuscript.

Conflict of interest There are no conflict of interest.

Ethical approval

Permissions to conduct the research was granted by the Ethiopian Wildlife Conservation Authority (permission no. EWCA Ref. No. 31/248/2010), and Mekelle University.

Research involving humans and/or animals participants Not applicable.
Consent to participate All authors gave consent to participate.
Consent for publication All authors gave consent for publication.

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Figures

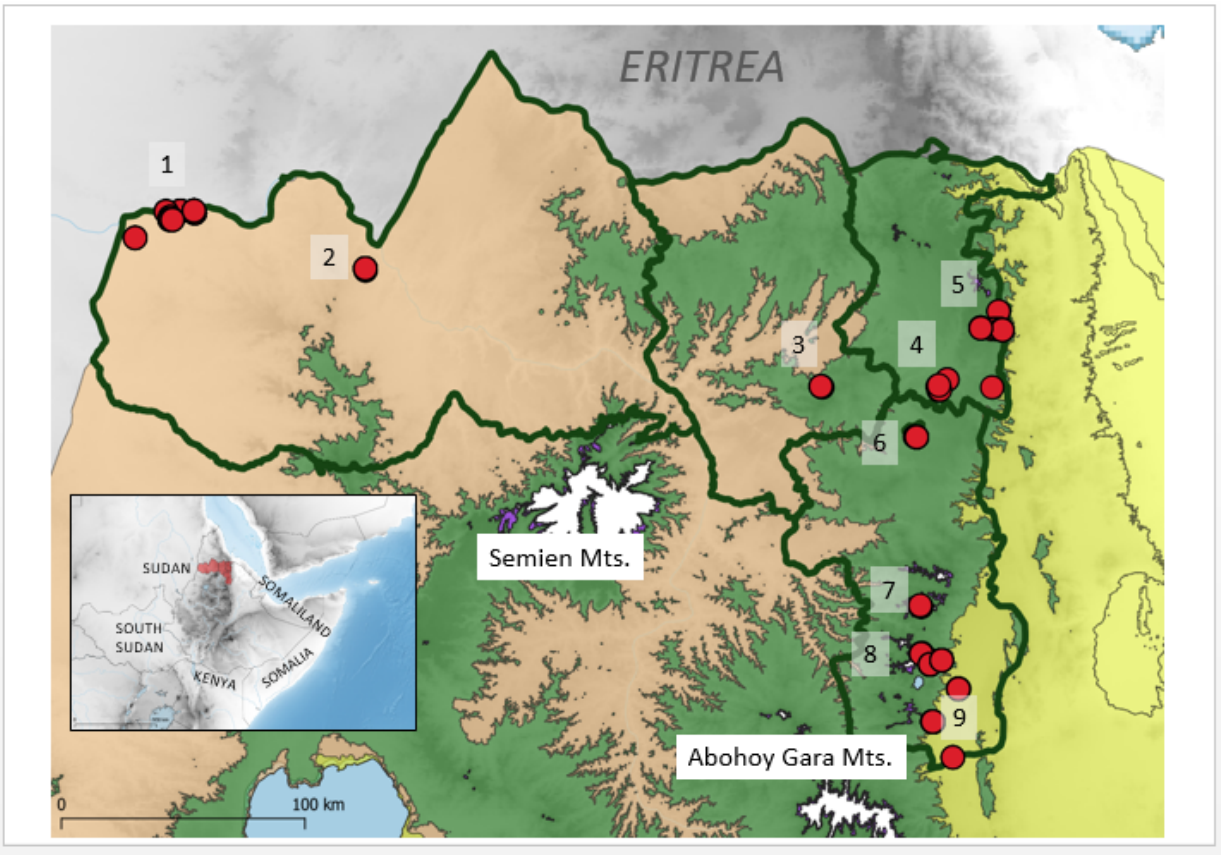

Figure 1

Distribution of major potential natural vegetation types in Tigray region, northern Ethiopia (based on Lillesø et al. 2011): AFROMONTANE MOSAIC (in green): Complex of Afromontane undifferentiated forest with wooded grasslands and evergreen or semi-evergreen bushland and thicket at lower margins. AFROALPINE HABITAT: Afroalpine vegetation (in white), Montane Ericaceous belt (in purple). SOMALI-MASAI SAVANNA (in yellow): Somalia-Masai Acacia (=Vachellia)-Commiphora deciduous bushland and thicket, Upland Acacia wooded grassland, Vachellia tortilis wooded grassland and woodland. SUDANIAN SAVANNA (in orange): Dry Combretum wooded grassland, Edaphic wooded grassland on drainage-impeded or seasonally flooded soils. WATER BODIES and wetlands are in blue. Inset shows the map of the Horn of Africa, where the study area (i.e. Tigray region) is shown in red colour (in the main figure, the borders of Tigray are marked by the dark green line). The sampling localities are indicated by red circles and grouped into regions numbered as follows: (1)

KSNP; (2) Mai-Temen; (3) Hagereselam; (4) Agula'e; (5) Atsbi; (6) Mekelle; (7) Mount Tsbet; (8) Hugumbrda-Grakahsu Forest; and (9) Raya Valley.

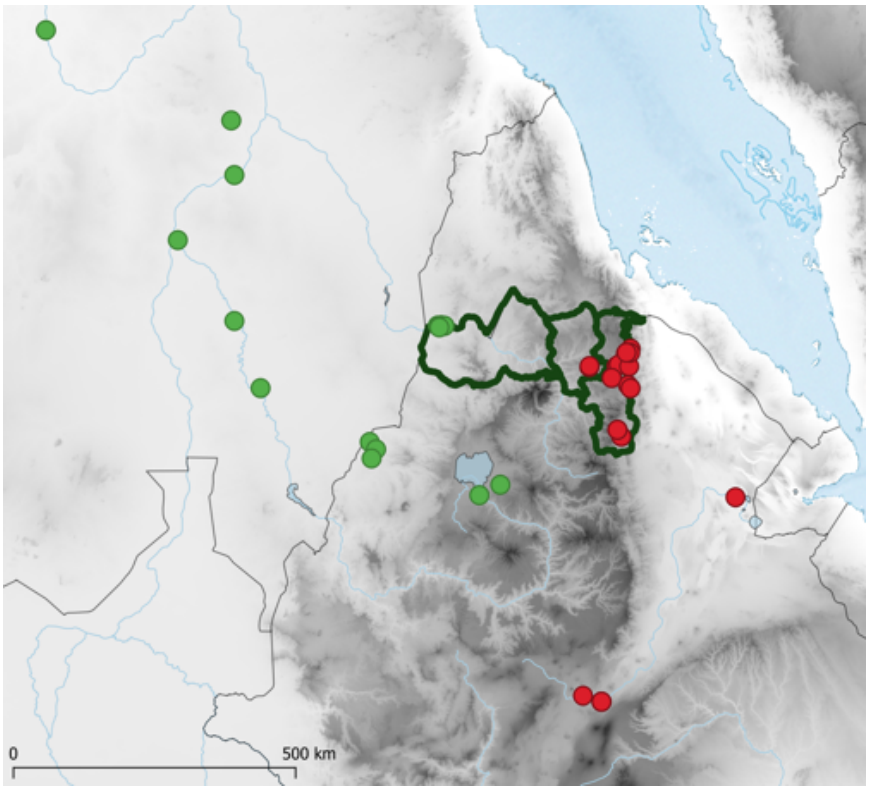

Figure 2

Distribution of genetic variability of Arvicanthis niloticus s. str. (sensu Bryja et al. 2019a; = C1 clade in Dobigny et al. 2013). The colours indicate two separate subclades: (red circle) found in the southern and eastern vegetation, and (green circle) in the western parts of the Tigray region. New data from Tigray were supplemented by sequenced specimens detailed in Bryja et al. (2019a) and Bryja et al. (2022).

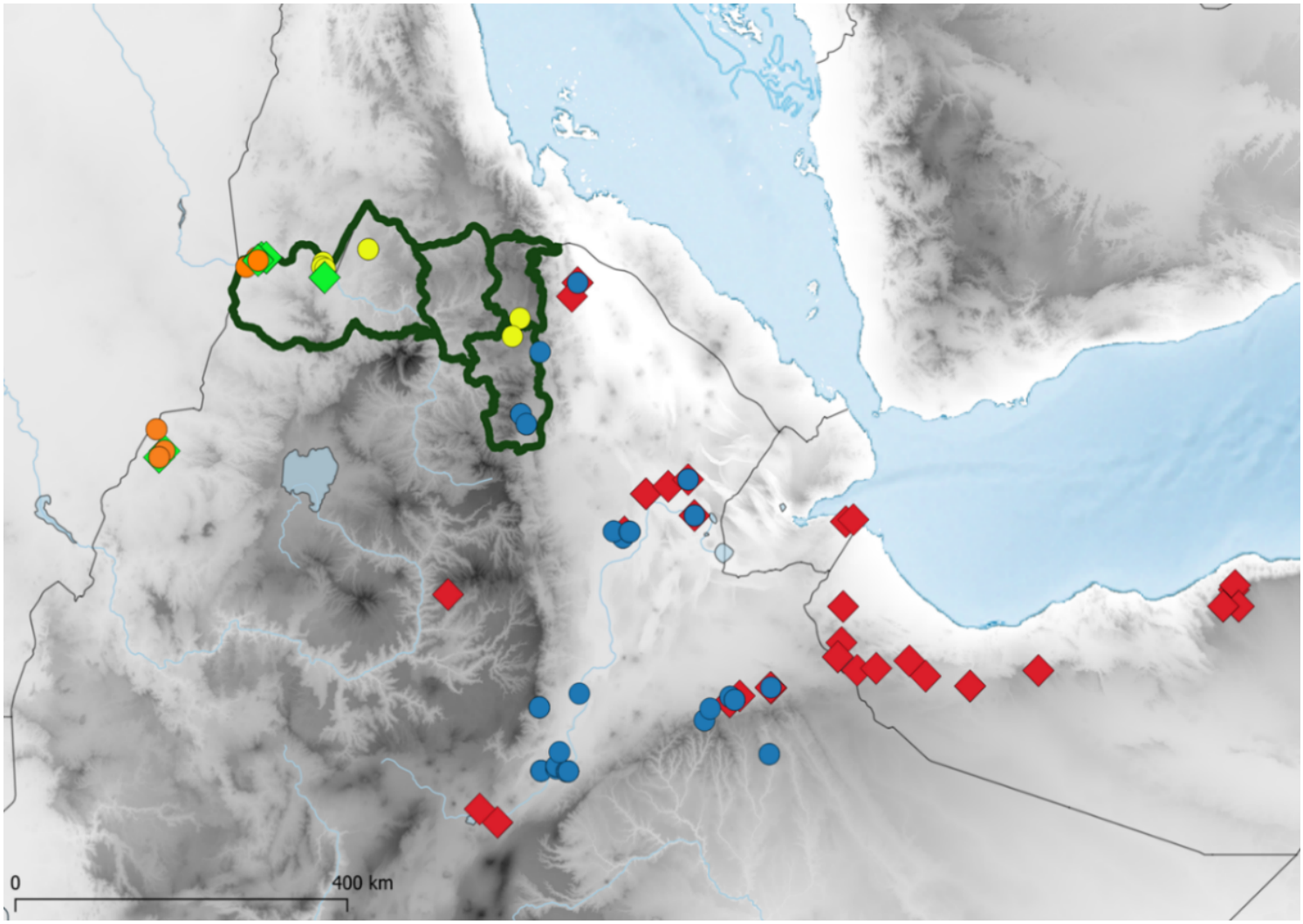

Figure 3

Known distribution of four species of *Acomys* occurring in Tigray: *Acomys mullah* (blue circles), A. sp. A (orange circle), A. sp. B (Green square), *A. cahirinus* (Yellow circle). *A. louisae* (red rhombuses) are endemic to the Afar Triangle (note that *A. louisae* has not yet been confirmed in Tigray, but its occurrence is very likely in low elevations along the border with Afar). New data from Tigray were supplemented by published data from Aghová et al. (2019), Frynta et al. (2020), and Bryja et al. (2022).

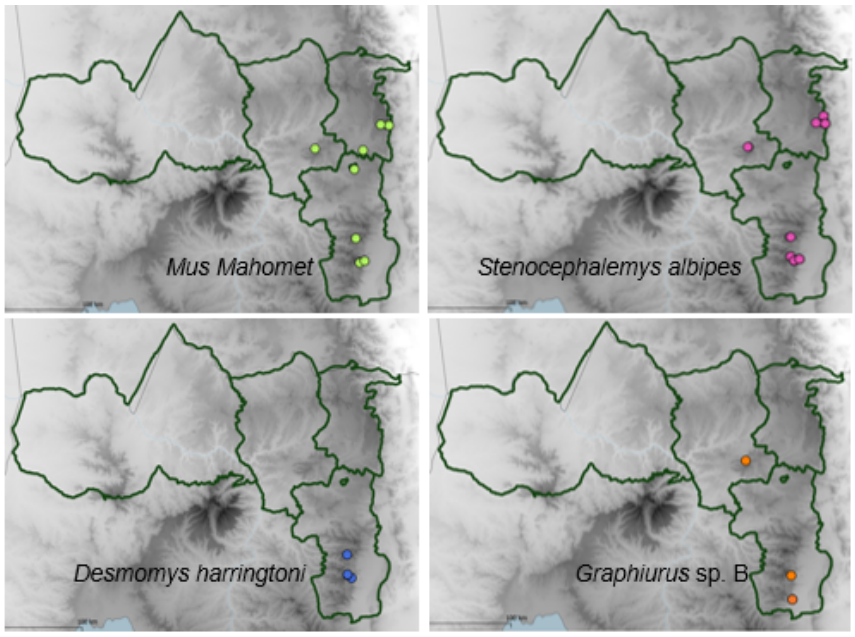

Figure 4

Distribution of four species of Ethiopian Highland endemics recorded in the Tigray region

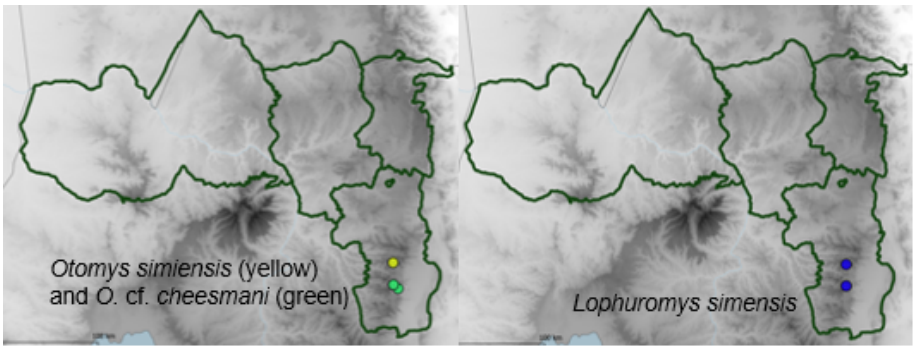

Figure 5

Distribution of two species of Ethiopian Highland endemics recorded in the Tigray region

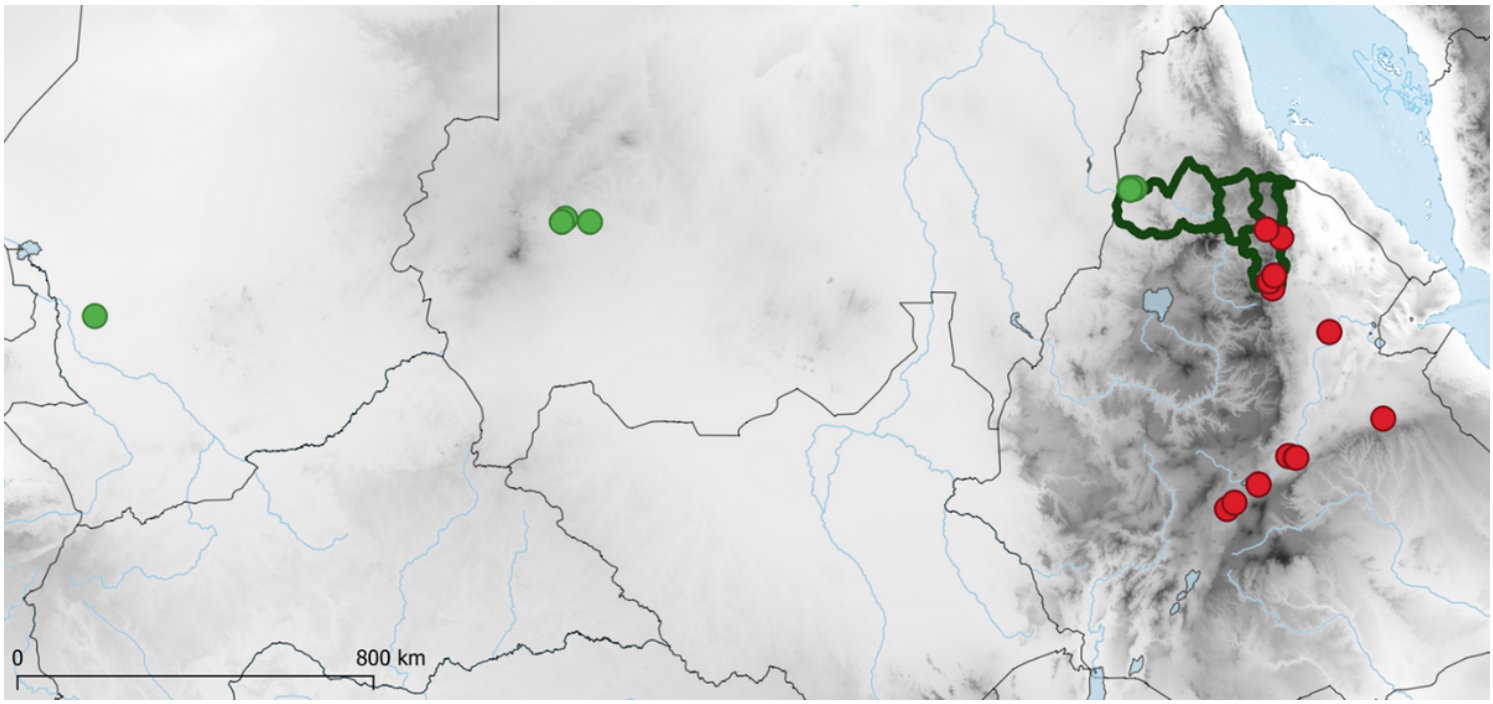

Figure 6

Distribution of genetic variability of *Gerbilliscus robustus*(sensu Aghová et al. 2017). Two deeply divergent haplogroups were discovered by Aghová et al. (2019): R1 (red circles) and R2 (green circles). New data from Tigray were supplemented by sequenced specimens detailed in Aghová et al. (2017) and Bryja et al. (2022).

Supplementary Files

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