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**COMMUNICATION**

**ECOLOGICAL NICHE MODELLING PREDICTS SIGNIFICANT IMPACTS OF FUTURE CLIMATE CHANGE ON TWO ENDEMIC RODENTS IN EASTERN AFRICA**

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Ecological niche modelling predicts significant impacts of future climate change on two endemic rodents in eastern Africa

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Abstract: The impact of climate change on rodents is well studied, however, many of these studies are restricted to the Americas. Small- to medium-sized rodents, especially murids, are restricted in their home range and microclimatic niche breadth, and are known to be more sensitive to changes in bioclimatic conditions over time. We analyzed the effect of future climatic scenarios in the near and distant future, using two global climate models (CanESM5 and MIROC-ES2L) for two shared socio-economic pathways (SSP2-4.5 and SSP5-8.5), on two eastern Africa endemic small-bodied mice: Stenocephalemys albipes and Mastomys awashensis. Our results indicate that while S. albipes showed increases in area of climatic suitability in the future, M. awashensis is predicted to suffer severe decline in the area of its fundamental niche.

Keywords: Awash Multimammate Mouse, Ethiopian White-footed Mouse, decline, microclimate, MaxEnt.

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Author contribution: All authors contributed equally to the study, analysis, and writing the manuscript.

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INTRODUCTION

Rodents are the most diverse and abundant groups of mammals, accounting for approximately 2,200 species (Monadjem et al. 2015), distributed across the world on every continent except Antarctica (Nowak 1999). They occur in a wide range of terrestrial habitats, and serve the purpose of ecosystem engineers (Zhang et al. 2003) and keystone species in an ecosystem. Africa supports a large diversity of rodent species, with at least 463 known species (Monadjem et al. 2015), and new species described regularly; however, the ranges and habitats of some rodent species in Africa are not clearly known, due to many reasons ranging from inaccessible localities to insufficient data or resources (Kingdon 1997; Habtamu & Bekele 2008; Takele et al. 2011). This is of especial concern as rodents are not only diverse, but are an integral part of the ecosystem’s functioning and health, contributing essential services (Fischer 2017). They are also of biogeographic, systematic, and conservation interest and priority (Happold 2013; Monadjem et al. 2015).

Rodents distributed in xerothermic habitats have been known to benefit from climate change towards a warmer, drier climate scenario, most likely due to their thermo-xerophilia being supported by the climatic conditions (Cameron & Scheel 2001). Climate change towards warmer and drier conditions has also resulted in an increase in species diversity in rodents in warm regions (Szpunar 2008). It is also possible that due to the effect of changing climate scenarios, migrations and emigrations take place, resulting in new regional populations being seeded and established in order to occupy the fundamental niche (Royer et al. 2016). As an extension of the conclusions drawn by Millien & Damuth (2004), treating fragmented populations as islands, it may be inferred that there is a possible slowing of the evolutionary rate of rodents as a result of climate change.

Hutchinson (1957) proposed the concept of the ‘ecological niche’ – an abstract representation of the biotic and abiotic factors deciding and limiting the distribution and abundance of a species. Identifying the ideal environmental niche of a species by accounting for certain limiting factors is one of the aims of ecological niche modelling (ENM) – this ideal niche is referred to as the fundamental niche (Griesemer 1994). The fundamental niche does not represent the real distribution of the species; in fact, it is usually larger than the realised distribution of the species (Soberón & Arroyo-Peña 2017). Ecological niche modelling uses presence-only or presence-absence occurrence data of a species and analyses it against a set of spatial covariates—most often, bioclimatic variables are used as the covariates in a climate change ENM study. Many diverse algorithms may be used for ENM, including generalised linear models (GLM), multivariate adaptive regression splines (MARS), and random forests (RF). MaxEnt (Phillips et al. 2006), however, is by far the most widely used algorithm due to its use of presence-only data, ease of access, customizability, and robustness (Ortega-Huerta & Peterson 2008; Elith et al. 2011; Merow et al. 2013; Radosavljevic & Anderson 2014).

The present study analyses the effect of current and future climate scenarios on the predicted fundamental niche of two Ethiopian-endemic rodents, the Awash Multimammate Mouse *Mastomys awashensis* (Lavrenchenko et al. 1998) and the Ethiopian White-footed Mouse *Stenocephalemys albipes* (Rüppell, 1842) (Image 1). It aims to predict the impact of future climate change pathways (SSP2-4.5 and SSP5-8.5) on the niches of these species using maximum entropy (MaxEnt) modelling.
MATERIALS AND METHODS

Study area
This study is based in Ethiopia and Eritrea, as both *Mastomys awashensis* and *Stenocephalemys albipes* are endemic to this region (Image 2). *M. awashensis* is distributed in the scrublands of the Awash River bank, which primarily comprises small Acacia and Commiphora trees and thorny scrubs, and is also found in agricultural fields and wild areas of the northern highlands (Lavrenchenko et al. 1998; Meheretu et al. 2014). *S. albipes* occur in moist montane forests, scrublands at high altitudes, and agricultural fields (Yalden & Largen 1992; Tilaye 2005; Kassa & Bekele 2008) (Image 2). The study region varies widely in altitude, geography, and climatic conditions, resulting in a high diversity of biological resources and high levels of endemism. The altitude of the region varies from 115m below sea level to 4,620m above sea level, and it can be classified into three climatic zones – tropical, subtropical, and cool. The mean annual temperature ranges 16–27 °C, and the annual precipitation ranges 510–1,280 mm. While the study is restricted to Ethiopia and Eritrea, the ecological niche modelling (ENM) was conducted on the entirety of continental Africa to account for ecological niche data outside the political borders of these countries; final models were then cropped to Ethiopia and Eritrea’s national boundaries.

Data collection
Occurrence data of the two study species were collected from Ethiopia and border regions in Eritrea. A total of 101 presence records were collected (34 for *M. awashensis* and 67 for *S. albipes*) from published literature (Lavrenchenko et al. 1998; Habtamu & Bekele 2008; Colangelo et al. 2010; Assefa & Srinivasulu 2019) and from GBIF (accessed August 2020) (Image 2; Appendix 1). Occurrence data of each species were spatially thinned using the package spThin (Aiello-Lammens et al. 2015) in R such that points within a 2km² area of each other were treated as duplicates and removed to account for spatial bias and autocorrelation.
in sample collection.

Nineteen bioclimatic environmental variables were acquired at a resolution of 2.5 arc-minutes from the Worldclim 2 database for the current time period (Fick & Hijmans 2017). For future scenarios, 2.5 arc-minute resolution data from the Coupled Model Intercomparison Project 6 (CMIP6) were acquired for two shared socioeconomic pathways - SSP2 representing a middle-of-the-road scenario (Fricko et al. 2017) and SSP5 representing fossil-fuelled development in the future (Kriegler et al. 2017). Two global climate models were used to account for inter-model disparities in projection (Porfrio et al. 2014) - MIROC-ES2L (Tachiiri et al. 2019a,b) and CanESM5 (Swart et al. 2019a,b). Data were acquired for the 2041–2060 (near future) and 2061–2080 (distant future) time periods.

An analysis of multicollinearity conducted using the package Virtualspecies (Leroy et al. 2015) in R version 4.0.2 (R Core Team 2020) was used to select relatively uncorrelated variables for the modelling. Variables with an absolute value of Pearson’s r >0.75 were subjected to pairwise comparisons of perceived ecological importance based on our understanding of the ecology and biology of the two species. All climate data were initially cropped to the extent of continental Africa; islands surrounding Africa including Madagascar were included, but southern Europe, the Middle East, and the Arabian Peninsula were not used.

Ecological niche modelling

A presence-only approach was used to model species distributions, using MaxEnt version 3.4.1 (Phillips et al. 2006); however, careful consideration of biases and selection of parameters is an essential step in order to maximise the robustness and reliability of niche models generated using MaxEnt (Derville et al. 2018). Hence, parameterisation was done according to the processes outlined in Merow et al. (2013) and Feng et al. (2019). To account for spatial bias, a Gaussian kernel density bias file of bandwidth 0.5 was created using the package SpatialEco (Evans 2020) in R, in order to weight the generation of background (pseudo absence) points for the analysis.

The model was parameterised for feature classes and regularisation multipliers using the package ENMEval (Muscarella et al. 2014). We tested a set of five regularisation multipliers: 0.5, 1, 2, 3, and 5, and six feature classes: Linear, Linear+Quadratic, Hinge, Hinge+Quadratic, Linear+Quadratic+Product, and Hinge+Quadratic+Product. Five-fold cross-validation was used and model performance was assessed using the area under the receiver operating characteristic curve (AUC) and the true skill statistic (TSS).

The continuous models for each scenario and each time period, as output by MaxEnt, were reclassified according to the maximum test sensitivity+specificity (MSS) threshold into binary models – the positive cells represented the fundamental niche of the species for each scenario and time period according to bioclimatic data. Finally, the binary models were cropped to Ethiopia and Eritrea’s national boundaries. Area of climatic suitability was calculated as a percentage based on the ratio of positive to zero cells in the final binary models.

RESULTS

Ecological niche modelling

For the modelling of both Mastomys awashensis and Stenocephalemys albipes, 12 bioclimatic layers were selected based on multicollinearity analysis (Appendix 2): BIO1 (Annual mean temperature), BIO2 (Mean diurnal range), BIO4 (Temperature seasonality), BIO5 (Maximum temperature of warmest month), BIO6 (Minimum temperature of coldest month), BIO8 (Mean temperature of wettest quarter), BIO9 (Mean temperature of driest quarter), BIO10 (Precipitation of driest month), BIO15 (Precipitation seasonality), BIO16 (Precipitation of wettest quarter), BIO18 (Precipitation of warmest quarter), and BIO19 (Precipitation of coldest quarter). After data cleaning and spatial thinning, 10 occurrence points were used for M. awashensis and 65 occurrence points were used for S. albipes. Models with the lowest Δ AICc values were selected as the final models for ENM analyses of each species – for M. awashensis this was Linear features with RM= 0.5 (Δ AICc= 0), and for S. albipes this was Linear+Quadratic features with RM= 0.5 (Δ AICc= 0). The models for M. awashensis and S. albipes returned AUC values of 0.974 ± 0.009 and 0.977 ± 0.011, respectively, and TSS values of 0.735 and 0.801, indicating robust performance for both species. Mean diurnal range and temperature seasonality had high contribution to the models of both species (Table 1).

Stenocephalemys albipes ENM

The ecological niche model for S. albipes (MSS threshold 0.525) showed that 20.704% of the study area is climatically suitable in the current time period (Image 3; Table 2). In both future time periods, scenarios, and GCMs, there was significant increase, with an average increase of 18.437% to 39.141 ± 3.695 % in 2041–2060,
and a further increase of 1.373% to 40.514 ± 5.035 % in 2061–2080. There was little difference in the percentage area of future climatic suitability between SSP2-4.5 and SSP5-8.5 (Image 3; Table 2), indicating that different future climate scenarios have little impact on the overall effect of climate change on this species.

The variables with the highest percentage contribution and permutation importance for this species were temperature seasonality (BIO4; 28% contribution, 38.8% p. imp.) and mean diurnal range (BIO2; 15.4% contribution, 12.8% p. imp.) (Table 1). Additionally, annual mean temperature (BIO1) had the highest percentage contribution to the model (41.2%), but showed 0 permutation importance, and similarly, mean temperature of the wettest quarter (BIO8) showed the highest permutation importance (44.2%), but had a very low percentage contribution to the model (0.9%).

In the current scenario, highest environmental suitability (>75%) according to climate was seen at a mean diurnal range (BIO2) of 14.901 ± 1.556 O°C, and a mean temperature seasonality (BIO4) of 114.903 ± 28.698 O°C. In SSP2-4.5, representing a middle-of-the-road scenario, BIO2 underwent a slight decrease to a mean value of 14.137 ± 1.139 O°C in the 2041–2060 time period, and further to 14.065 ± 1.185 O°C in 2061–2080; BIO4, however, increased to a mean value of 116.249 ± 33.281 O°C in 2041–2060, and further to 123.561 ± 39.416 O°C in 2061–2080 (Table 3).

**Mastomys awashensis ENM**

The ecological niche model for *M. awashensis* (MSS threshold 0.777) showed that 46.077% of the study area is climatically suitable in the current time period (Image 4; Table 2). In both future time periods, scenarios, and

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**Table 1. Variable contributions of each bioclimatic layer used in the analysis, for both species.**

| Variable | Name | Stenocephalemys albipes | Mastomys awashensis | Stenocephalemys albipes | Mastomys awashensis |
|----------|------|-------------------------|---------------------|-------------------------|---------------------|
| BIO1     | Annual mean temperature | 41.2 | 0 | 0 | 0 |
| BIO2     | Mean diurnal range | 15.4 | 27.7 | 12.8 | 18.2 |
| BIO4     | Temperature seasonality | 28 | 47.6 | 38.8 | 74.2 |
| BIO5     | Max temperature of warmest month | 0.1 | 0 | 0 | 0 |
| BIO6     | Min temperature of coldest month | 0.1 | 3.8 | 0.6 | 1.1 |
| BIO8     | Mean temperature of wettest quarter | 0.9 | 12.1 | 44.2 | 3 |
| BIO9     | Mean temperature of driest quarter | 2 | 0.2 | 0.4 | 0.5 |
| BIO14    | Precipitation of driest month | 0.5 | 1.9 | 0.4 | 2 |
| BIO15    | Precipitation seasonality | 0.6 | 1 | 1.4 | 0.9 |
| BIO16    | Precipitation of wettest quarter | 0.5 | 0.6 | 0.6 | 0.6 |
| BIO18    | Precipitation of warmest quarter | 0.8 | 2.6 | 0.8 | 0.3 |
| BIO19    | Precipitation of coldest quarter | 9.9 | 2.4 | 0 | 0.1 |

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**Table 2. Changes in climatically suitable areas of both species (in percentage values).**

| Scenario      | Time Period      | CanESM5 | MIROC-ES2L | Scenario      | Time Period      | CanESM5 | MIROC-ES2L |
|---------------|------------------|---------|------------|---------------|------------------|---------|------------|
| SSP2-4.5      | 2041–2060        | 0%      | 0%         | SSP2-4.5      | 2041–2060        | 39.982  | 34.527     |
| SSP2-4.5      | 2061–2080        | 0%      | 0%         | SSP2-4.5      | 2061–2080        | 40.113  | 35.353     |
| SSP5-8.5      | 2041–2060        | 0%      | 0%         | SSP5-8.5      | 2041–2060        | 43.462  | 38.594     |
| SSP5-8.5      | 2061–2080        | 0%      | 0%         | SSP5-8.5      | 2061–2080        | 47.407  | 39.186     |
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GCMs however, there was complete and total decline, resulting in 0% of the study area being climatically suitable by 2041–2060 and into the future (Image 4). This indicates that *M. awashensis* is extremely sensitive to climate change scenarios, and due to the effect of climate change alone, will lose all of its fundamental niche in the near future.

For this species, temperature seasonality (BIO4; 47.6% contribution, 74.2% p. imp.) and mean diurnal range (BIO2; 27.7% contribution, 18.2% p. imp.) were the highest contributors (Table 1). All the other variables had significantly lower percentage contribution and permutation importance.

In the current scenario, highest environmental suitability (>75%) according to climate was seen at a mean diurnal range (BIO2) of 15.986 ± 1.075 °C, and a mean temperature seasonality (BIO4) of 136.481 ± 33.077 °C (Table 3).

| Stenocephalemys albipes | Scenario | Time Period | BIO2 | BIO4 |
|--------------------------|----------|-------------|------|------|
| Current                  | 14.901 ± 1.556 | 114.903 ± 28.698 |
| SSP2-4.5                 | 2041–2060 | 14.137 ± 1.139 | 109.902 ± 30.14 |
| SSP5-8.5                 | 2041–2060 | 109.902 ± 30.14 | 14.065 ± 1.185 |
| SSP2-4.5                 | 2041–2060 | 14.065 ± 1.185 | 111.027 ± 32.032 |
| SSP5-8.5                 | 2041–2060 | 111.027 ± 32.032 | 14 ± 1.171 |
| SSP2-4.5                 | 2061–2080 | 14 ± 1.171 | 116.249 ± 33.281 |
| SSP5-8.5                 | 2061–2080 | 116.249 ± 33.281 | 13.572 ± 1.258 |
| SSP2-4.5                 | 2061–2080 | 13.572 ± 1.258 | 123.561 ± 39.416 |
| SSP5-8.5                 | 2061–2080 | 123.561 ± 39.416 | 14.935 ± 1.318 |

| Mastomys awashensis | Scenario | Time Period | BIO2 | BIO4 |
|---------------------|----------|-------------|------|------|
| Current             | 15.986 ± 1.075 | 136.481 ± 33.077 |
DISCUSSION

Ecological niche models have often been used to model and project rodent distributions and niches, but a large proportion of these studies are restricted to species found in the Americas (Martínez-Salazar et al. 2012; Bean et al. 2014; Kubiak et al. 2017; Flores-Zamarripa & Fernández 2018; Urbina-Cardona et al. 2019; Pardi et al. 2020). African rodents have also been studied using ENM techniques; Taylor et al. (2015) showed that trends in the distribution of Afromontane rodents reflect changes in biomes predicted by past, present, and future climate scenarios. McDonough et al. (2015) showed in a hindcasting-based study on the Bushveld Gerbil (Gerbilliscus leucogaster) in Zambesi, that it is significantly impacted by changing climatic scenarios, but this was not explored in terms of future climate change. A general ecological niche model fitted by Martinov et al. (2020) created an estimation of the current predicted distribution of Mastomys species, including *M. awashensis*, however this analysis did not estimate the fundamental niche through binary modelling, and there was no projection to future climate scenarios.

Our results are in agreement with the findings of Martinov et al. (2020), where the current distributions show high likelihood (>0.8) in areas included under our predicted current fundamental niche. Our results also emphasise the importance of ecological niche modelling and future projection of ENM analyses, due to the severity of the impact of climate change on *M. awashensis* (Ortega-Huerta & Peterson 2008).

The two species in our study—*Mastomys awashensis* and *Stenocephalemys albipes*—show significant changes as a result of changing climate scenarios. The result of our study for *S. albipes* shows a percentage area of current climatic suitability of 20.704%, with an increase of 18.437% in the near future (2041–2060), and a further increase of 1.373% in the distant future (2061–2080) in both climatic scenarios. Despite the different perspectives SSP2-4.5 and SSP5-8.5 take in terms of socioeconomic scenarios, emissions, and concentrations of greenhouse gases, there was negligible difference between the two in the future predictions of the fundamental niche of this species, suggesting that while climate change positively impacts this species, there is little impact of specific climate pathways. This result is in line with conclusions drawn by McDonough et al. (2015), where it was shown that rodent niches expanded from the last glacial maximum (approximately 200,000 years BP) through the last interglacial period (approx. 130,000 to 118,000 years BP), to the present day, most likely due to increasing temperatures across the year. The decrease in predicted future mean diurnal range most suitable for this species when compared to the current time period shows that in both shared socioeconomic pathway scenarios, this species will favour slightly colder climates. This effect is very small, however, as the largest change in mean diurnal range is from current to the 2061–2080 time period, with a 1.329 ± 0.298 °C decrease.

In the case of *M. awashensis*, the current niche is relatively large, with 46.077% appearing to be climatically suitable for this species; however, it appears to be incredibly sensitive to climate change events, as in all future scenarios and time periods, none of the study area (and also the rest of Africa) appeared to be climatically suitable. This is a massive and drastic change, which reflects the high sensitivity of this species to climate change. Seasonal variation in temperature and mean diurnal range of temperature are the most important predicting factors for this species, which leads to the inference that this species is likely to be most affected by temperatures getting generally warmer and less seasonally varied, which happens in both scenarios.

According to the MaxEnt model, both species had relatively wide areas of climatic suitability (Images 3, 4). For both species, the northern regions of Ethiopia and parts of southern Eritrea were climatically suitable—this included highland, some lowland regions of the Great Rift Valley, and some scattered sites in southeastern Ethiopia. *S. albipes* had climatically suitable regions in the highlands of northern, western, and central Ethiopia, including Tigray, Amhara, northern Oromia, Southern Nations, Nationalities, & Peoples’ (SNNP), Addis Ababa, and eastern Benishangul-Gumuz regions. There are also some scattered suitable sites near Harari in Ethiopia, and Debub and Gash-Barka regions in Eritrea. In all future scenarios and time periods, this species’ fundamental niche was seen to expand and move westward in Ethiopia and Eritrea, occupying the Tigray, Amhara, Benishangul-Gumuz, Oromia, Addis Ababa, Gambela, and SNNP regions in Ethiopia & Gash-Barka and Debub regions in Eritrea. Some scattered areas of suitability were also seen in the Eritrean & Ethiopian highlands and in the highlands south of Dire Dawa. *M. awashensis* showed climatic suitability in Tigray, Amhara, eastern Benishangul-Gumuz, Oromia, SNNP, Addis Ababa, Harari, and some parts of northern Somali regions. In Eritrea, it showed high climatic suitability in Gash-Barka and Debub. For both species, the Eritrean and Ethiopian highlands formed a distinct geographical
barrier, and no areas of climatic suitability were present east of the hill range. Earlier studies of both species have shown them to be restricted to highland habitats (Corti et al. 2005; Mohammed et al. 2010; Meheretu et al. 2014), however, some later studies reported them to occur from lowlands as well (Habtamu & Bekele 2008; Lavrenchenko et al. 2010). Our study corroborates these with our current predicted niche expanding to lowland regions as well as highlands.

The results of the present study show the efficacy of ecological niche modelling in offering important insights into the potential geographic distributions of African rodents. Although M. awashensis is present and has areas of climatic suitability in protected areas, it is likely that there are no species-specific conservation measures in place. The eventual increase in anthropogenic impact on the natural areas will only decrease the chances of the species’ survival in the future, as the impact of climate change alone is very large. It is important to plan ground-truthing of the sites shown as part of the fundamental niche of both this study’s species in order to ascertain their true distribution, range, and realised niche, as this will help create better conservation strategies. It is imperative that species-specific conservation measures are set in place based on the results of said ground-truthing, including in situ conservation management, captive breeding, and planned reintroductions.

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Appendix 1. Localities used in ENM analysis of *Stenocephalemys albipes* and *Mastomys awashensis*.

| Name                        | Latitude | Longitude | Locality                      | Reference                        |
|-----------------------------|----------|-----------|--------------------------------|----------------------------------|
| *Stenocephalemys albipes*   | 5.800    | 39.200    | Kebre Mengist, Ethiopia        | GBIF                             |
|                             | 6.217    | 37.667    | Dega Done, Gemu-Gofa, SNNP, Ethiopia | Demeke et al. 2007               |
| *Stenocephalemys albipes*   | 6.233    | 37.567    | Mt Dorse, Chenckia, Gemu-Gofa, SNNP, Ethiopia | GBIF                             |
| *Stenocephalemys albipes*   | 6.383    | 38.583    | Kebre Mengist, Sidamo, Ethiopia | GBIF                             |
| *Stenocephalemys albipes*   | 6.833    | 40.550    | Jebo Samo, Bale, Ethiopia      | GBIF                             |
| *Stenocephalemys albipes*   | 6.917    | 39.167    | Gedeb Mts., Ethiopia           | GBIF                             |
| *Stenocephalemys albipes*   | 6.983    | 40.020    | 7 km SE of Goga, Bale, Ethiopia | GBIF                             |
| *Stenocephalemys albipes*   | 7.050    | 39.167    | Webi river, north of Dodola, Arsi, Ethiopia | GBIF                             |
| *Stenocephalemys albipes*   | 7.100    | 39.767    | Webi river, W of Dinshu, Bale, Ethiopia | Zerihun et al. 2012              |
| *Stenocephalemys albipes*   | 7.117    | 39.733    | 5 km W of Dinshu, Bale, Ethiopia | GBIF                             |
| *Stenocephalemys albipes*   | 7.133    | 39.717    | Mount Gaysay, Bale, Ethiopia   | GBIF                             |
| *Stenocephalemys albipes*   | 7.134    | 36.954    | Gorka Bera, Chebera-Churchura NP, Ethiopia | Demeke & Afework 2014            |
| *Stenocephalemys albipes*   | 7.433    | 35.000    | Godare forest, Tepi, Ethiopia  | Lavrenchenko 2017                 |
| *Stenocephalemys albipes*   | 7.580    | 38.000    | Seka, 3 Km N Of, Horo, Ethiopia | GBIF                             |
| *Stenocephalemys albipes*   | 7.600    | 38.450    | Alage, Ethiopia                | Agerie & Afework 2015            |
| *Stenocephalemys albipes*   | 7.620    | 36.770    | Buyo Kechema, Ethiopia         | GBIF                             |
| *Stenocephalemys albipes*   | 7.650    | 36.800    | Jiren Farm, Jimma, Ethiopia    | Fadesse & Afework 2012            |
| *Stenocephalemys albipes*   | 7.667    | 39.333    | Albasso forest, Ethiopia       | GBIF                             |
| *Stenocephalemys albipes*   | 7.750    | 36.730    | Atro, Agaro, Ethiopia          | GBIF                             |
| *Stenocephalemys albipes*   | 7.820    | 36.680    | Agaro, 14 km by road SE of Mejo, Ethiopia | GBIF                             |
| *Stenocephalemys albipes*   | 7.833    | 39.333    | Wodajo, Ethiopia               | GBIF                             |
| *Stenocephalemys albipes*   | 7.917    | 39.283    | Jawi Chilalo, Galama mtn, Arsi, Ethiopia | Mohammed et al. 2010             |
| *Stenocephalemys albipes*   | 7.917    | 39.450    | Mt Albasso, Camp Wodajo, Ethiopia | GBIF                             |
| *Stenocephalemys albipes*   | 8.155    | 35.525    | Illubabor, W of Gore, Ethiopia | GBIF                             |
| *Stenocephalemys albipes*   | 8.183    | 35.367    | Lemen, Ethiopia                | GBIF                             |
| *Stenocephalemys albipes*   | 8.250    | 36.167    | Yemenigist Den Yebaja Chaka, Ethiopia | GBIF                             |
| *Stenocephalemys albipes*   | 8.280    | 36.900    | Atenago, Ethiopia              | GBIF                             |
| *Stenocephalemys albipes*   | 8.367    | 35.817    | Wabo, 5 km of W of Scechhi river, Ethiopia | GBIF                             |
| *Stenocephalemys albipes*   | 8.500    | 34.775    | Addo, 7km SW of Dembidolo, Ethiopia | GBIF                             |
| *Stenocephalemys albipes*   | 8.517    | 39.200    | Wonji Sugarcane, Qoboluto Tumsa, Ethiopia | Serekebirhan et al. 2011         |
| *Stenocephalemys albipes*   | 8.917    | 38.583    | Dima Goranda, Ethiopia         | GBIF                             |
| *Stenocephalemys albipes*   | 9.017    | 35.250    | Sido Were Wele, Ethiopia       | GBIF                             |
| *Stenocephalemys albipes*   | 9.050    | 38.520    | Berfeta Lemefa, near Holetta, Ethiopia | GBIF                             |
| *Stenocephalemys albipes*   | 9.067    | 38.650    | Mersagesha forest, Shoa, Ethiopia | Afework 1996                     |
| *Stenocephalemys albipes*   | 9.117    | 37.050    | Bako, Shoa, Ethiopia           | GBIF                             |
| *Stenocephalemys albipes*   | 9.517    | 38.217    | Subagajo, Ethiopia             | GBIF                             |
| *Stenocephalemys albipes*   | 10.333   | 37.833    | Debra Markos, Gojam, Amhara, Ethiopia | Ejigu & Afework 2013             |
| *Stenocephalemys albipes*   | 10.494   | 39.611    | Yetere forest, Ethiopia        | Gezahegn et al. 2016             |
| *Stenocephalemys albipes*   | 10.667   | 37.917    | Nazret M Alem, Ethiopia        | GBIF                             |
| *Stenocephalemys albipes*   | 10.739   | 36.800    | Ardity forest, Awi zone, Ethiopia | Gstachow & Afework 2015          |
| *Stenocephalemys albipes*   | 10.846   | 38.675    | Borena-Sayint NP, Ethiopia     | Meseret & Solomon 2014           |
| *Stenocephalemys albipes*   | 11.117   | 37.317    | Amedamit Mount, Amhara, Ethiopia | GBIF                             |
| *Stenocephalemys albipes*   | 11.167   | 36.250    | Pawe area, B. Gumuz, Ethiopia  | Tilahun et al. 2012              |
| Name                        | Latitude | Longitude | Locality                          | Reference                          |
|-----------------------------|----------|-----------|------------------------------------|------------------------------------|
| Stenocephalemys albipes     | 11.267   | 36.833    | Dangila, Amhara, Ethiopia          | GBIF                               |
| Stenocephalemys albipes     | 11.417   | 37.967    | Shime, Ethiopia                    | GBIF                               |
| Stenocephalemys albipes     | 11.583   | 37.417    | Bihar-Dar, Amhara, Ethiopia        | GBIF                               |
| Stenocephalemys albipes     | 11.717   | 37.917    | Mahdere Marayam, Gondar, Amhara, Ethiopia | GBIF                               |
| Stenocephalemys albipes     | 12.350   | 35.783    | Alatish NP, Ethiopia               | Tadesse & Aferwork 2008             |
| Stenocephalemys albipes     | 12.617   | 37.483    | Gondar, Amhara, Ethiopia           | GBIF                               |
| Stenocephalemys albipes     | 12.633   | 37.500    | NE of Angereb Dam, Gondar, Amhara, Ethiopia | GBIF                               |
| Stenocephalemys albipes     | 12.750   | 37.700    | Yerer mountain forest, Shoa, Ethiopia | Yonas & Fikresilasie 2015           |
| Stenocephalemys albipes     | 13.133   | 37.917    | Debark, NE Gondar, Amhara, Ethiopia | GBIF                               |
| Stenocephalemys albipes     | 13.133   | 37.917    | Semien Mts, Amhara, Ethiopia       | GBIF                               |
| Stenocephalemys albipes     | 13.192   | 37.933    | Debir, Ethiopia                    | GBIF                               |
| Stenocephalemys albipes     | 13.232   | 38.038    | Semien NP, Ethiopia                | GBIF                               |
| Stenocephalemys albipes     | 13.650   | 39.172    | Hagereselam, Ethiopia              | Meheretu et al. 2012                |
| Stenocephalemys albipes     | 14.166   | 37.309    | Habesha Adi Goshu, Ethiopia        | GBIF                               |
| Stenocephalemys albipes     | 14.183   | 37.305    | Kunama Adi Goshu, Ethiopia         | GBIF                               |
| Stenocephalemys albipes     | 14.210   | 36.766    | Adebayetown, Ethiopia              | GBIF                               |
| Stenocephalemys albipes     | 14.251   | 37.270    | Kunama Adi Goshu, Ethiopia         | GBIF                               |
| Stenocephalemys albipes     | 14.284   | 36.688    | Kafta-Sheraro NP, Tigray, Ethiopia | Alembrhan & Srinivasulu 2019       |
| Stenocephalemys albipes     | 14.291   | 36.677    | Helet Coka, Ethiopia               | GBIF                               |
| Stenocephalemys albipes     | 14.950   | 38.270    | Mt. Kullu, Shambiko, Eritrea       | GBIF                               |
| Stenocephalemys albipes     | 15.332   | 39.064    | Nefasit, Eritrea                   | GBIF                               |
| Stenocephalemys albipes     | 11.083   | 36.850    | Aquatimo forest, Gojjam, Ethiopia  | GBIF                               |
| Mastomys awashensis         | 9.000    | 40.167    | Awash, Ethiopia                    | GBIF                               |
| Mastomys awashensis         | 7.833    | 38.717    | S of Zway Lake, Ethiopia           | GBIF                               |
| Mastomys awashensis         | 8.383    | 39.150    | E of Koka Lake, Bati Qelo, Ethiopia| GBIF                               |
| Mastomys awashensis         | 9.065    | 42.275    | Nigaya Bobasa, Babile Sanctuary, Ethiopia | GBIF                               |
| Mastomys awashensis         | 13.668   | 39.175    | Hagereselam, Ethiopia              | GBIF                               |
| Mastomys awashensis         | 12.600   | 39.517    | N of Lake Hashenge, Ethiopia       | MBG & Dessalegn 2015               |
| Mastomys awashensis         | 14.210   | 36.766    | Near Adebaye Town, Kafta Sheraro National Park, Ethiopia | Alembrhan & Srinivasulu 2019       |
| Mastomys awashensis         | 14.251   | 37.270    | Kunama Adi Goshu, Kafta Sheraro National Park, Ethiopia | Alembrhan & Srinivasulu 2019       |
| Mastomys awashensis         | 14.284   | 36.688    | Helet Coka, Ethiopia               | GBIF                               |
| Mastomys awashensis         | 14.287   | 36.679    | Adebaye Geter, E of Himora, Ethiopia| GBIF                               |
| Mastomys awashensis         | 14.184   | 37.305    | NW of Birkuta, Ethiopia            | GBIF                               |
| Mastomys awashensis         | 14.168   | 37.310    | Habesha Adi Goshu, Ethiopia        | GBIF                               |
| Mastomys awashensis         | 7.2545   | 36.798    | Gojob River, Ethiopia              | GBIF                               |
| Mastomys awashensis         | 14.213   | 37.322    | Shebe, Ethiopia                    | GBIF                               |
| Mastomys awashensis         | 7.6011   | 36.500    | Gibe National Park, Ethiopia       | GBIF                               |
| Mastomys awashensis         | 8.2334   | 37.5823   | Gibe National Park, Ethiopia       | GBIF                               |
| Mastomys awashensis         | 8.4657   | 39.1606   | Lake Koka, Bati Qelo, Ethiopia     | GBIF                               |
| Mastomys awashensis         | 8.6943   | 36.149    | Didessa River, Ethiopia            | GBIF                               |
| Mastomys awashensis         | 8.8453   | 40.0119   | Awash National Park, Ethiopia      | GBIF                               |
| Mastomys awashensis         | 9.0586   | 42.2796   | Babile Elephant Sanctuary, Ethiopia| GBIF                               |
| Mastomys awashensis         | 9.1478   | 42.2624   | Babile Elephant Sanctuary, Ethiopia| GBIF                               |
| Mastomys awashensis         | 9.2249   | 34.8662   | Dhati-Welel National Park, Ethiopia| GBIF                               |
| Name                  | Latitude | Longitude | Locality                          | Reference               |
|-----------------------|----------|-----------|-----------------------------------|-------------------------|
| Mastomys awashensis   | 9.2393   | 34.8653   | Dhati-Welel National Park, Ethiopia | Martynov et al. 2020    |
| Mastomys awashensis   | 9.2449   | 34.8644   | Dhati-Welel National Park, Ethiopia | Martynov et al. 2020    |
| Mastomys awashensis   | 9.5548   | 39.7818   | Ankober, Ethiopia                  | Martynov et al. 2020    |
| Mastomys awashensis   | 9.5554   | 39.7657   | Ankober, Ethiopia                  | Martynov et al. 2020    |
| Mastomys awashensis   | 11.0526  | 39.6481   | Kombolcha, Ethiopia               | Martynov et al. 2020    |
| Mastomys awashensis   | 11.7525  | 37.9068   | Gumara River, Ethiopia             | Martynov et al. 2020    |
| Mastomys awashensis   | 11.7797  | 37.7313   | Gumara River, Ethiopia             | Martynov et al. 2020    |
| Mastomys awashensis   | 12.5492  | 39.6431   | Adi Mancarre, Ethiopia             | Martynov et al. 2020    |
| Mastomys awashensis   | 12.6393  | 39.5383   | Adi Aba Musa, Ethiopia             | Martynov et al. 2020    |
| Mastomys awashensis   | 12.6551  | 39.5816   | Kube, Ethiopia                     | Martynov et al. 2020    |
| Mastomys awashensis   | 13.1858  | 37.9671   | Simien Mts National Park, Ethiopia | Martynov et al. 2020    |
| Mastomys awashensis   | 14.0945  | 37.4575   | Mai-Temen, Ethiopia                | Martynov et al. 2020    |
Appendix 2. Correlation matrix resulting from the spatial multicollinearity test of the 19 bioclimatic variables used in the analysis.

| Layer | BIO1 | BIO2 | BIO3 | BIO4 | BIO5 | BIO6 | BIO7 | BIO8 | BIO9 | BIO10 | BIO11 | BIO12 | BIO13 | BIO14 | BIO15 | BIO16 | BIO17 | BIO18 | BIO19 |
|-------|------|------|------|------|------|------|------|------|------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| BIO1  | 1.000 |      |      |      |      |      |      |      |      |       |       |       |       |       |       |       |       |       |       |
| BIO2  | -0.031 | 1.000 |      |      |      |      |      |      |      |       |       |       |       |       |       |       |       |       |       |
| BIO3  | 0.141  | -0.489 | 1.000 |      |      |      |      |      |      |       |       |       |       |       |       |       |       |       |       |
| BIO4  | -0.116 | 0.567  | -0.951 | 1.000 |      |      |      |      |      |       |       |       |       |       |       |       |       |       |       |       |
| BIO5  | 0.633  | 0.554  | -0.604 | 0.666 | 1.000 |      |      |      |      |       |       |       |       |       |       |       |       |       |       |       |
| BIO6  | 0.681  | -0.599 | 0.745  | -0.766 | -0.123 | 1.000 |      |      |      |       |       |       |       |       |       |       |       |       |       |       |
| BIO7  | -0.120 | 0.769  | -0.906 | 0.958  | 0.688  | -0.805 | 1.000 |      |      |       |       |       |       |       |       |       |       |       |       |
| BIO8  | 0.744  | 0.128  | 0.134  | -0.128 | 0.471  | 0.486  | -0.074 | 1.000 |      |       |       |       |       |       |       |       |       |       |       |
| BIO9  | 0.516  | -0.258 | -0.074 | 0.116  | 0.405  | 0.330  | -0.053 | 1.000 |      |       |       |       |       |       |       |       |       |       |       |
| BIO10 | 0.754  | 0.312  | -0.501 | 0.556  | 0.957  | 0.077  | 0.516  | 0.496  | 0.561 | 1.000 |      |       |       |       |       |       |       |       |       |
| BIO11 | 0.775  | -0.399 | 0.701  | -0.713 | 0.022  | 0.969  | -0.695 | 0.578  | 0.326  | 0.186  | 1.000 |      |       |       |       |       |       |       |       |
| BIO12 | -0.051 | -0.627 | 0.767  | -0.776 | -0.660 | 0.555  | -0.800 | -0.076 | -0.051 | -0.534 | 0.464  | 1.000 |      |       |       |       |       |       |       |
| BIO13 | 0.042  | -0.513 | 0.718  | -0.769 | -0.565 | 0.574  | 0.758  | -0.002 | -0.055 | 0.452  | 0.527  | 0.920  | 1.000 |      |       |       |       |       |       |       |
| BIO14 | -0.079 | -0.478 | 0.463  | -0.377 | -0.400 | 0.303  | -0.461 | -0.063 | -0.002 | -0.303 | 0.185  | 0.571  | 0.334  | 1.000 |      |       |       |       |       |       |
| BIO15 | 0.425  | 0.282  | 0.092  | -0.180 | 0.246  | 0.274  | -0.053 | 0.490  | -0.064 | 0.210  | 0.393  | -0.154 | -0.111 | -0.402 | 1.000 |      |       |       |       |       |
| BIO16 | 0.004  | -0.501 | 0.716  | -0.762 | -0.585 | 0.543  | -0.747 | -0.029 | -0.075 | 0.479  | 0.496  | 0.937  | 0.991  | 0.352  | 0.070  | 1.000 |      |       |       |       |
| BIO17 | -0.077 | -0.530 | 0.507  | -0.421 | -0.436 | 0.342  | 0.510  | -0.072 | 0.017  | 0.329  | 0.215  | 0.626  | 0.378  | 0.984  | -0.428 | 0.394 | 1.000 |      |       |       |
| BIO18 | -0.170 | -0.513 | 0.610  | -0.637 | -0.633 | 0.376  | 0.653  | -0.035 | -0.244 | 0.571  | 0.272  | 0.805  | 0.713  | 0.536  | -0.150 | 0.728  | 0.577 | 1.000 |      |       |       |
| BIO19 | 0.070  | -0.461 | 0.456  | -0.417 | -0.338 | 0.404  | 0.486  | -0.074 | 0.185  | -0.383 | 0.335  | 0.631  | 0.547  | 0.418  | -0.208 | 0.562  | 0.454 | 0.279 | 1.000 |      |       |       |
