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The Effect of Soil Physical Properties and Soil Microclimate on Rodent Burrows' Abundance and their Characteristics in Western Usambara Mountains, Tanzania

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Authors' contributions

This work was carried out in collaboration between all authors. Author JLM designed the study, wrote the protocol, conducted field work, performed statistical analysis, and wrote the first draft of the manuscript. Author LB designed the study, conducted field work, author BHJM, designed, conducted field work, author DNK designed, conducted field work, managed the literature searches and edited drafts. Author BMM designed the study, conducted field work and edited drafts. Authors LSM, NIK, JAD, HG, and HL designed the study and edited drafts. All authors read and approved the final manuscript.

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ABSTRACT

The present study was carried out between September 2009 and June 2013 in Western Usambara Mountains plague focus with the aim of establishing the influence of selected soil physical properties and soil microclimate on rodent burrows' abundance, portal orientation and use. Two landscapes with high and medium plague frequencies in Lokome and Lukozi villages were studied. In the two landscapes data were collected from 117 and 200 observation sites respectively, using 100 m x 200 m quadrats. At each quadrat crossing, a sample quadrat of 20 m x 20 m was demarcated for scanning rodent burrows whereby burrows encountered were counted and their portal orientation and burrow use described. Within each sample quadrat, selected soil physical properties including thickness of the soil genetic horizons and soil dry consistence were determined. Soil samples were collected from each horizon for laboratory texture analysis. Temperature (surface and subsurface to a depth 10 cm) and relative humidity at a depth of 10 and 30 cm were collected using infrared, thermo-couple thermometers and *i*-Buttons. Descriptive statistics, ANOVA and logistic regression were used to analyse the data by R-software. There were significant (*P*=.0001) differences between the two landscapes regarding topsoil depth, infrared temperature, relative humidity and rodent burrows' abundance. In the high plague frequency landscape there was a significant influence (*P*=.05) of topsoil horizon thickness on rodent burrows' abundance and use. Results also indicate that soil temperature to a depth of 10 cm was significantly (*P*=.05) correlated with rodent burrow use. Likewise, in the medium plague frequency landscape, soil physical properties and soil microclimate significantly (*P*=.0001) discouraged rodent burrowing. It was concluded that soil physical and soil microclimate encouraged and discouraged burrowing in the high and the medium plague frequency landscapes, respectively. The landscape with high rodent burrows' abundance corresponded with high plague frequency records.

Keywords: Rodent burrows; burrows' abundance; soil microclimate; soil physical properties; plague focus.

1. INTRODUCTION

Soils are a habitat for rodents, which are burrowing mammals [1]. Soils are important for burrow making by most fossorial and subterranean small mammals [2,3]. Soil types and soil microclimate are reported to determine burrows' density in certain areas [4,5]. Research conducted in Morogoro, Tanzania, has shown that soil texture influences population growth of *Mastomys natalensis* in agricultural farms [6]. Other studies have shown that soil and soil microclimate influence distribution of rodents through their influence on habitats and food resources distribution [7].

It has been established that most rodent habitats are determined by multiple factors, among them being vegetation cover [8], food availability [7] soil types [6], topography and slope gradient [9 & 10] and soil and microclimate [11]. Soil and soil related factors like texture and moisture have been reported to be strong determinants of rodent burrowing [12]. Rodent burrows are the proxy of rodent populations which have been linked to human plague outbreaks in Western Usambara Mountains [13,14]. Similar observations were reported when studying relationships between climate and the frequency of human plague in the South-Western USA [15].

Rodent burrows offer a favourable environment for growth and increased rodent populations due to availability of supportive conditions for harbouring and safeguarding of young rodents. Literature indicates that burrows provide security and encouraging environment for population growth of both rodents and fleas [7,10]. Abiotic factors have been reported to influence burrows' abundance. The key abiotic factors established to influence abundance of rodents include soil temperature, soil moisture and soil organic matter [3&16]. Literature indicates that rodents have a number of preferences in relation to abiotic components for the specific location of their burrows; soil type has a significant influence on the spread and abundance of rodents [9,10,17]. Soil microclimate, which is a function of soil type and micro-geographical features, is another important influencing parameter on the distribution of rodent burrows. Climatic variables affecting soil properties, such as temperature and soil moisture, may change suitability of an area for rodent species [18]. It has been reported too that climate determines the burrows' architecture and portal orientation such that portals are oriented towards the sunlight and sun rays' direction, and away from incoming winds [19–21]. Other researchers indicated that soil moisture and food availability to rodents encourage burrows' repair and burrowing activities and use [19]. Therefore, exploring these factor may improve understanding of predicting where rodent burrow abundance are, the information that offer means of estimating the rodent population for monitoring and surveillance before reach outbreak levels, and hence manage them.

However, studies that explored the influence of soil physical properties and soils' microclimate on rodent burrows' density and their characteristics are few. Recent studies in the Western Usambara Mountains partially confirmed the above hypothesis [17]. It is envisaged that exploration of rodent burrows' relationship with soil physical properties and soil microclimate could enlighten on why there are differences of historical plague frequency between the neighbouring villages, the fact that previous studies did not. For example some researches indicated there is a gradient of plague occurrence forming two categorical landscapes which are the high and medium plague frequency corresponding to Lokome and Lukozi landscapes [22-26]. The objective of the current study was to find out the influence of soil physical properties and soil microclimate on burrows' abundance in Western Usambara Mountains, Tanzania.

2. MATERIALS AND METHODS

2.1 Description of the Study Area

The study was carried out in Western Usambara Mountains, northeastern Tanzania between September 2009 and June 2013. The area is located within Universal Transverse Mercator (UTM) Zone 37, UTM 9474 965 N through 9502586 N and 444532E through 472276E. Two sample areas (Lokome and Lukozi) were selected based on two criteria. The first one is historical plague reported incidence levels (high, medium and low). The high plague frequency landscape had plague cases that range from 4.2–10.5 per 1000 inhabitants and medium ranges from 1.9–4.2 plague case per 1000 inhabitants. Second criterion used to delineate these landscapes is differences in landform setting and farming systems, climatic variability and landform. The high plague frequency landscape is located at an elevation of 1800-2100 metres above mean sea level (amsl), whereas the medium plague frequency landscape is located between 1770 and 1890 metres amsl.

The climate of Western Usambara Mountains is characterised as "warm temperate with dry winter and warm summer". The two areas are located in the rain shadow of Magamba ridge. Temperatures are variable where annual average ranges between 15ºC and 17ºC for the high and medium plague frequency areas respectively and a relative humidity average recorded stands at 70%. The areas receive almost similar amounts of rainfall in two seasons with slight variation from 500 to 800 mm and 600 to 900 mm per annum for the high and medium plague frequency, respectively. The rainfall pattern is weakly bimodal where short rains start in October to December, but with moisture deficit and long rains start in March through end of May. The rainfall onset and distribution are unreliable. Rainfall onset and distribution influence human activities and even water resources and food availability to small mammals, and hence their habitation.

Crops grown are common in both areas, but intensities and land sizes differ. Also, the position cultivated on the landform varies between the areas and so are the yields per hectare. The dominant food crops grown include maize (*Zea mays*), cassava (*Manihot esculenta*), sweet potato (*Ipomoea batatas*), banana (*Musa* species.), round potato (*Solanum tuberosum*) and various beans (*Phaseolus* species). Cash crops include assorted vegetables like cabbage (*Brassica oleracea*), tomato (*Solanum lycopersicum*) and carrot (*Daucus carota*) and various fruits such as pears, plums and apples. Crop cultivation is carried out mostly on slopes and on relatively narrow U-shaped valley bottoms where traditional irrigation is practised [27,28].

2.2 Determination of Soil Physical Properties

Soils were studied along pre-determined grids' centres by augering to a depth 120 cm or to an obstructing layer. Also were studied by mini-pit to a depth of 100 cm and by representative soil profile pits which were dug to a depth of 200 cm. Soils were described using the FAO guidelines for soil profile description [29]. Measurements were made for landform characteristics such as elevation (metres amsl), slope gradient (%) and also estimated rockiness and surface stoniness as percent coverage. Also, soil depth was determined by tape measure (cm) following the genetic horizons of soil profile, while soil dry consistence was measured by the feel method at specified depth of 0-30 cm, 30-60 cm and >60 cm for dry soil consistence dry1, dry2 and dry3, respectively, using qualitative method (soft, slightly hard, hard and very hard) as indicated in FAO guidelines [29]. Soil samples were analysed for texture by hydrometer method [30]. The sampling plots were at a crossing of quadrats of 100 m by 200 m along and across the slope. There were a total of 117 and 200 quadrats for high and medium plague frequency corresponding to Lokome and Lukozi landscapes, respectively. Different lengths of quadrats were used because the landforms were more variable along the slope than across.

2.3 Determination of Soil Microclimate

Microclimate is any climatic condition in a relatively small area, within a few metres or less above and below the earth's surface and within canopies of vegetation. It is influenced by temperature, relative humidity, wind and evaporation. In this study soil temperature and soil relative humidity were considered. The soil surface and subsoil temperatures and relative humidity (%) of subsoil at 10 and 30 cm depths were measured near the small mammal's burrow at the grid's centre. The depth of 30 cm was opted for because most rodent burrows in the Western Usambara Mountains are that deep [17]. Three instruments were used to assess soil temperature, each at a time. These were Fluke 66 (infrared) thermometer, Eijkelkamp K-thermo-couple and i-Buttons. The Fluke 66 infrared thermometer is a simple device that was used to directly read surface soil temperature by switching on the thermometer to radiate infrared signals on the soil surface which were translated into digital readings of soil temperature in degrees Celsius. Measurements were taken at random around auger holes. Shady places and green vegetation were avoided. Another thermometer was an Eijkelkamp K-thermo-couple which was used to measure the subsoil temperature at 10 cm in degrees centigrade. The soil temperature readings were in each case taken at similar places where the surface temperature was taken and a total of five measurements were taken around the burrow.

The soil temperature and relative humidity (%) were also measured using i-Buttons. Due to their smaller size and that they could be misplaced in the soil, iButtons were tied with a piece of mosquito net, being a material that would not influence temperature and relative humidity readings. The i-Buttons were then inserted in two soil depths which were 10 and 30 cm using a tied mosquito net in a drilled auger hole. The auger holes were filled up with soil from the same auger hole and soft soil mass from the surrounding area without rough particles or plant materials. The i-Buttons were set for three consecutive days, because this was assumed to be enough duration to capture existing soil temperature (in °C) variation in that season and it allowed easy transfer of i-Buttons to other data collection sites; they were dug up and data were transferred to the computer via data logger.

2.4 Determination Rodent Burrows' Abundance

Grids of 100 m down the slope and 200 m across the slope were used to identify and study rodent burrows. In order to capture all rodent burrows in the grid with minimal errors and avoid bias, smaller grids of 20 m x 20 m were designated within the larger grids. Data collected included the number of rodent burrows, the use or non-use and burrows' portal orientation towards main slope descent.

2.5 Data Analysis

Comparative data analysis for the two sites was done using descriptive statistics where statistical parameters: Mean, median, mode and standard deviations were compared. Scatter plots and correlation were used to explore the data for multicollinearity and normality before One-Way ANOVA and regression analyses were performed. The One-way ANOVA [31] was used to assess if the differences of means of landforms, soil physical properties and soil microclimate attributes between high and medium plague frequency landscapes were statistically significant.

Regression analysis was carried out using Generalized Linear Models (GLM) family binomial and multinomial, to identify strong attributes that explain rodent burrows' abundance and difference between the high and medium plague frequency landscapes. The GLM technique was adopted because it is suitable for regression modelling of distribution when the variance is not constant, and/or when the errors are not normally distributed [32] and when the dependent variable is binary (i.e. Yes, No, or 0, 1) [31] which applies to the data. The GLM procedure was implemented through a graphical user interface (GUI) library (Rattle) [33] that was operated in R-software, version R i386 3.0.0. Data sets used were small mammal burrows' abundance (presence/absence), burrow orientation and burrow use (0, 1) which were dependent (y) variables while the independent variables were soil depth (cm), textural particles (sand%, silt% and clay%), soil surface and subsoil temperature, dry soil consistence and soil relative humidity at two depth 10 and 30 cm. Categorical variables (burrow orientation and dry consistence) were assigned dummy codes. In fitting the GLM, distribution family was "Bernoulli" and link "Logit" for binary dependent variables and multinomial for multiple dependent variables were used [31]. Validation was done by data portioning whereby 70 % was used for training and 30% for model development. Multicollinearity was addressed by entering weakly correlated variables serially in the model. Variables were put in the model or removed by checking variance inflation factors and checking the magnitude of error. Developed models were selected by picking the model with a smaller Akaike Information Criterion (AIC) [34].

3. RESULTS AND DISCUSSION

3.1 Differences of Landform Characteristics and Rodent Burrows' Abundance in the Two Plague Affected Landscapes

It was established that in the high plague frequency landscape where 117 grids were examined there were 389 rodent burrows out of which 10 had 109 fleas and 12 ticks, whereas in the medium plague frequency landscape, where 200 grids were studied, there were 100 rodent burrows and no fleas in any of the burrows. Table 1 presents results of landform characteristics and surface attributes and rodent burrows' abundance in the two plague affected areas of West Usambara Mountains.

3.2 Differences of Landform Attributes, Soil Physical Properties and Soil Microclimate between High and Medium Plague Frequency Landscapes

ANOVA results show that there were statistically significant (*P*=.0001) differences in elevation (metres amsl), slope gradient (%), surface rocks and stones, soil texture, herbaceous plant cover, topsoil depth (cm) and the number of rodent burrows between the high and medium plague frequency landscapes. Also, there were significant (*P*=.0001) differences between surface soil temperature (infrared), soil thermocouple (10 cm depth) and relative humidity at 30 cm soil depth. Results further show significant (*P*=.0001) differences between the two landscapes for vegetation cover where there was more cover in the high plague frequency landscape because of existing forest plantations and nature reserve, and most areas of the adjoining escarpment had long time fallows.

On the other hand in the medium plague frequency landscape which is below 1800 metres amsl, vegetation cover was comparatively low compared to the high plague frequency landscape, although there were woodlots and few trees planted along farm boundaries and around homesteads (Table 1). The high plague frequency landscape also experiences the wind currents blowing from the lower plains hence regulating temperatures at the altitude above 1900 metres amsl. The fact that there were more burrows in the high plague frequency landscape than in the medium plague frequency landscape (Table 1) may imply that soil temperatures and relative humidity were more favourable for rodents' habitation [11,18] in the high than in the medium plague frequency landscape, giving insight as to why there are plague frequency differences between the two landscapes [35]. Further it has been shown that elevation and human disturbances which were different in the two landscapes of Western Usambara Mountains also strongly influence spatial rodent distribution and hence their burrows [36]. In addition, research carried out along the slopes of Mount Kilimanjaro indicated that elevation and vegetation were major factors influencing spatial distribution and diversity of rodents [37].

Therefore, the higher number of rodent burrows in the high than in the medium plague frequency landscapes could be attributed to the differences in heterogeneity between the two landscapes. The results show that the landscape variability was prominent in the high than in the medium plague frequency landscape (Table 1). The high plague frequency landscape is characterised by more steep slopes, rocks, stones and herbaceous cover which appeared to influence greatly rodent habitation. Therefore, the high plague frequency landscapes had higher rodent burrows' abundance, which correspond with reported human plague frequency [22-26,38]. These results agree well with report that rodents prefer establishing their habitation in favourable environment where risk of predators is low and

Table 1. Rodent burrows' abundance, slope gradient, surface rocks/stones and herbaceous cover in the high and medium plague frequency landscapes

	High	Medium	High	Medium	High	Medium	High	Medium	High	Medium	High	Medium
Statistics	**Slope gradient (%)**		**Surface rocks**		**Surface stones**		**Herb cover**		**topsoil depth (cm)**		**Rodent burrow numbers**	
Count (n)	(117)	(194)	(117)	(200)	(117)	(200)	(117)	(200)	(116)	(200)	(117)	(201)
Mean	40.0	21.9	16.3	0.13	14.3	0.1	9.5	2.6	18.9	23.2	3.4	0.5
Median	29.0	23.0	0	0	0	0	1.0	0.0	15.0	20.0	1.0	0.0
SD	48	12.0	27.2	1.2	24.1	0.5	18	12	10.0	11.4	4.7	1.6
Minimum	2.0	0.5	0	0	0	0	0	0	3.0	2.0	0.0	0.0
Maximum	500	61	90	15	90	5	80	90	50	70	25	13

where water and food resources are available [2,7]. It has been reported too that rodent burrows are selectively placed along steep slopes in upland and never in lowland [10]. Rodents also make burrows out of evolutionary behavioural complexities developed by genetics [39].

This implies that there may be differences that are based on local environment surrounding rodent populations. The two landscapes have different endowments, the high plague frequency landscape being more favoured than the medium plague frequency landscape.

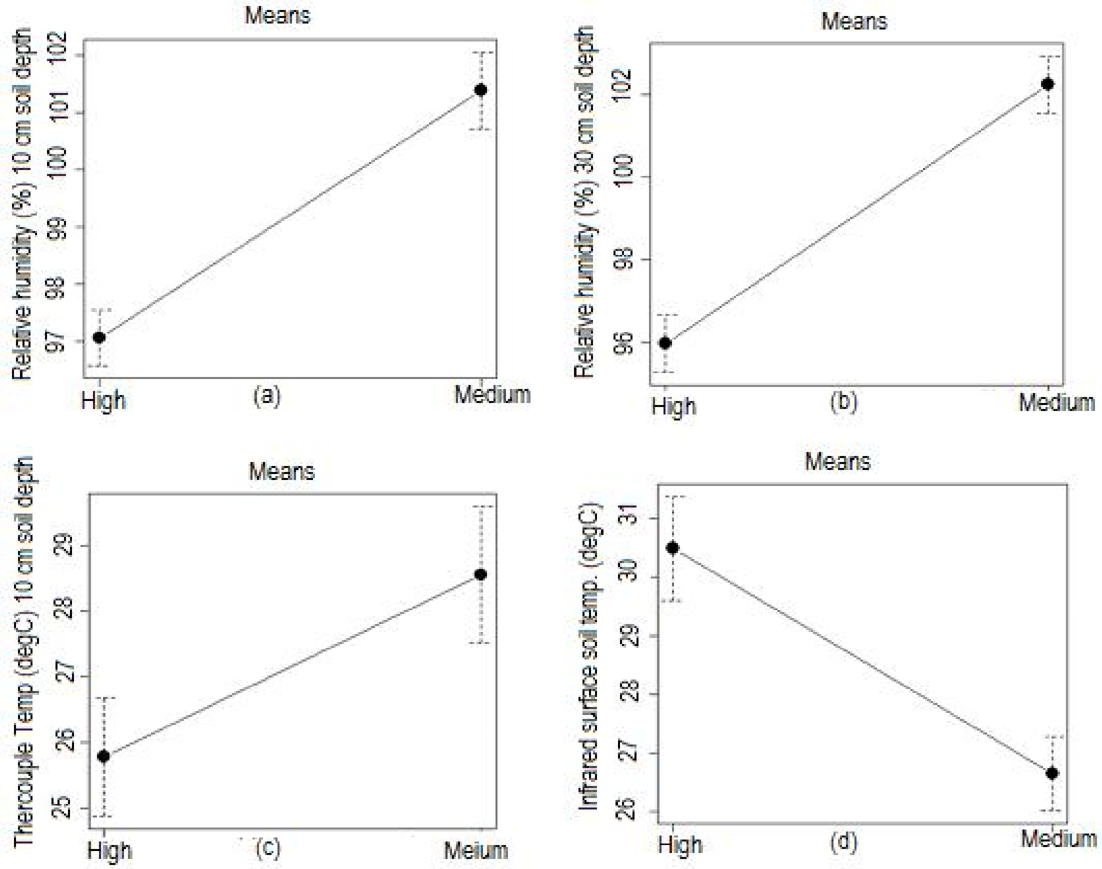
Results further show that there were differences of burrows' abundance in different slope aspect. In the high plague frequency landscape, slopes facing south-west (SW), North (N) and north-west (NW) had 94 (24.6 %), 67 (17.4%) and 53 (13.7 %) rodent burrows, respectively while in the medium plague frequency landscape, slope facing Southeast (SE), Northeast (NE) and West (W) had 30 (32.6%), 26 (28.3%) and 15 (16.3%) rodent burrows, respectively. This means rodent burrows in the high plague frequency landscapes were mostly pointing westwards (38%) whereas in the medium plague frequency they were mostly pointing eastwards (61%). The above result signifies the importance of burrows' portals orientation. Other researchers have shown that small mammals orient burrows' portals to slope aspects facing solar incoming radiation to light and warm inside [19-21] or just certain direction which create favourable burrow condition [10].

The orientation of the rodent burrows' portals although meant to warm rodent burrows by orienting away from the wind in cold season and towards the wind in hotter season [20] it also helps the vectors (fleas to survive because they are ecto-thermic hence sensitive to temperature fluxes and usually develop from larvae to adult off the host i.e. the burrows' temperature becomes the only way of survival [40]. This means that the different soil temperatures in the two landscapes favour the vector differently. In places where temperature and relative humidity are high like the case of the medium plague frequency landscape, the environment favours fungal growth which destroys the flea larvae. It has been documented that fleas (the plague vectors) can only survive where temperatures and relative humidity are optimal for survival [40,41] and this partly depends on how the burrow portal is oriented towards sunlight and or wind [20]. This might be among explanations as to why there are differences of plague outbreak in the two studied landscapes, that there are differences in burrows' abundance between the two landscapes, whereby the one with fewer burrows (medium plague frequency landscape) had no fleas; while the one with high rodent burrows' abundance (high plague frequency landscape) had fleas in 15% of the counted burrows. This corresponds well with the historical plague outbreaks in the area hence soil microclimate could be among factors explaining the observed plague frequency differences.

Fig. 1 (a-d) presents results of mean plots of relative humidity (RH %), surface soil temperature (infrared) and the K-thermo-couple temperature at different depths. The results show differences between the high and medium plague frequency landscapes. The differences are statistically significant (P=.0001) for relative humidity (RH) (%) in 30 cm depths. However, the 10 and 30 cm depths for RH had higher values in the medium plague frequency landscape than in the high plague frequency landscape (Fig. 1 a & b). Results also show that K-thermo-coupe temperature is significantly (P=.0001) higher in the medium than in the high plague frequency landscape (Fig. 1c). In the case of infraded surface temperature, higher values are observed in the high plague frequency landscape than in the medium plague frequency landscape. Generally, the high infrared surface soil temperature could be attributed to the dense presence of rocks and stones which were significantly (P=.0001) higher in the high than the medium plague frequency landscape. These rocks and stones heatup during the day time consequently elevating surface temperature.

The high K-thermo-couple temperature and relative humidity (%) could be attributed to the landform setting, land use and topsoil depth. Results show that there were statistically significant (P=.0001) differences between the two plague affected landscapes for elevation and slope gradient, and these may have influenced the amount of solar energy the different landscapes receive. Again, the medium plague frequency landscape has been deforested and seasonally cleared extensively for cultivation thereby allowing sunshine to illuminate over the surface directly and the solar energy absorbed and stored in the soil, making the soils warmer. However, in the high plague frequency landscape with more vegetation cover (plantation forestry, natural forest) and steep slopes, these reduce the amount of solar radiation the area receives by covering the surface and also smaller angle reduces solar radiation effectiveness. The compounded effects of vegetation cover and angle of inclination reduces solar energy trapped, which ultimately may compromise with soil temperature in the area. Additionally, the high relative humidity levels in the medium plague frequency landscape could be attributed to topsoil depth which was significantly (P=.0001) deeper and with less stones and rocks than the topsoil depth in the high plague frequency landscape. It could also be attributed to the nature of slopes of the landscape which allow rainfall infiltration which provokes more rock and soil parent material weathering than in the steep and short slopes in the high plague frequency landscapes.

Table 2 presents the results of dry consistence between two landscapes. The results show that the topsoils were harder (consistence dry 1 and dry 2) in the high plague frequency landscape as compared to soft and lightly hard consistence observed in the medium plague frequency landscape. The dry consistence difference between the landscapes was not significant, but the high plague frequency landscape was generally more compacted. Research findings elsewhere have shown that soil hardness negatively influence burrowing as rodents avoid using much energy to dig in hard places [42]. However, if there is no softer place and no alternative hiding caves, rodents make burrows even in hard places but the network and complexities may be different [2].



Key: High = high plague frequancy landscapes
Medium = medium plague frequency landscapes

Fig. 1. Soil temperature and relative humidity in the high and medium plague frequency landscapes, Westen Usambara Mountains, Tanzania

3.3 Generalized Linear Model (GLM) regression analysis

3.3.1 Influence of soil physical properties and soil microclimate on rodent burrows' abundance in the high plague frequent landscapes

Table 3 shows the influence of soil physical properties, temperature and relative humidity attributes on burrows' abundance. Topsoil depth (Depth1, 0-30 cm), which is a natural Ap/Ah horizon [29], was a statistically significant ($P<.05$) soil physical property for prediction of burrows' abundance, with a relative influence of 39.5 %.

This implies that thick ≤ 30 cm Ap (topsoils Ap depth in cm) encourages rodent burrowing. The average thickness of topsoil (Table 1) in which the rodent burrows were located in this study are in line with a report that rodent burrows are limited to topsoils, at depths of 10–45 cm [5], but this may vary with soil types whereby in sandy soils burrows can go as deep as 190 cm [43] and seasons and type of rodents [4,5]. These results also agree well with other researchers who indicated that rodents prefer topsoils for burrowing because they are well drained [21,44], loose and easy to make burrows without using much energy as compared to cohesive and compact subsoils [44–48].

3.3.2 Influence of soil physical and soil microclimate to rodent burrows' portals orientation in high plague frequency landscapes

Table 4 presents results indicating that there was no statistically significant influence of soil physical properties and soil microclimatic attributes on rodent burrow portal orientation. This would mean that the considered attributes were not good predictor variables with regard to rodent burrows' portals orientation.

3.3.3 Influence of soil physical properties and soil microclimate attributes on burrows' use in the high plague frequency landscape

Table 5 presents results showing that topsoil depth, Ap/Ah horizon (topsoils Ap depth in cm) and sub-soil temperature were statistically significant ($p<.05$) in influencing rodent burrow use with relative influence of 28.8 and 32.8 per cent. This would mean that both soil depth and subsoil-temperature encourage burrow use. This could be attributed to the topsoils' textures which are mainly sandy clay loams, well drained, slightly harder; so do not collapse easily, hence preferable by burrowing and use.

The results agree with previous research which indicated that rodents make and prefer burrows for security, nursing the young ones, for storage of food and for cushioning from weather fluxes [2,7]. Soil types impact the depth at which burrows are set. Literature shows that in sandy soils rodent burrows are very deep whereas in clayey soils they are shallow and complex and difficult to make [43,49]. It has been reported that rodents makes burrows where the energy use is minimal [47]. In the studied landscapes, the burrows' depths were mainly within 30 - 45 cm soil surface.

3.3.4 Influence of soil physical properties and soil microclimate attributes on burrows in the medium plague frequency area

Table 6 presents results on coefficients' estimates, direction of influence and standard error of predictors. Results show statistical significance ($P<.05$) for the topsoil dry consistence (consistence dry1), subsoil dry consistence (ConsDry2) and subsoil relative humidity (RH (%) 30 cm) to influence burrows' abundance in the medium plague frequency landscape. While the topsoil dry consistence encourages burrowing, the subsoil relative humidity discourages burrowing. These results suggest that burrows are likely to be more abundant in relatively harder and less humid topsoils, than in soft and moist top soils.

The negative influence of relative humidity on rodent burrows' abundance could be attributed to the requirement by rodents to disperse heat, which is compromised in the high relative humidity environment [50]. Research elsewhere has shown that rodents prefer to make burrows in soft, well drained soils in order to reduce thermal stress and the cost of burrow making [19,51]. The reason is that rodents are homeothermal (they are animals that maintain body temperature at a constant level) and need to regulate their body temperature through evaporation, which is highly reduced when relative humidity is high [2,7,50]. Further, relative humidity has been illustrated as key to flea survival because the larvae are susceptible to desiccation and in excessive relative humidity attacked by fungi [40]. Other reports show that because most of the life cycle of flea is in the rodent burrows the distribution and pattern of fleas can be determined by the habitat differences and in particular the surrounding microclimate [52].

Table 2. Differences in dry soil consistence in the studied plague affected landscapes

Statistics	**High plague frequency**			**Medium plague frequency**		
	Consistence dry 1	**Consistence dry 2**	**Consistence dry 3**	**Consistence dry 1**	**Consistence dry 2**	**Consistence dry 3**
Mean	1.3	1.4	1.2	1.1	1.3	1.2
Median	1	1	1	1	1	1
STD	0.59	0.62	0.93	0.38	0.60	0.69
Skewness	1.61	0.84	0.46	1.31	1.25	0.53
Minimum	1	1	1	1	1	1
Maximum	3	3	4	2	3	3
n	117	117	117	200	200	200

Key: Consistence dry: 1=soft; 2=slightly hard, 3=hard, 4=very hard

Table 3. Soil physical properties and soil microclimate factors explaining burrows' abundance in the high plague frequency landscapes

Variable	**Constant/ estimate**	**Std. error**	**z value**	**Pr(>|z|)**
(Intercept)	-0.34	13.159	-0.026	0.979
Depth1 (0 -30 cm)	0.119	0.0829	1.442	0.015*
Depth2 (30-60 cm)	0.010	0.0522	0.185	0.854
Depth3 (>60 cm)	-0.005	0.0302	-0.16	0.873
Consistence Dry1 (0-30 cm)	1.395	1.3679	1.02	0.308
Consistence Dry2(30-60 cm)	-0.436	1.2023	-0.363	0.717
Consistence Dry3 (>60 cm)	0.391	0.8062	0.485	0.628
Infrared Temperature (Celsius)	-0.049	0.0685	-0.724	0.469
Thermal Couple (10cm)	0.068	0.0451	1.522	0.128
Relative humidity (%)_10cm	-0.108	0.1166	-0.931	0.352
Relative humidity (%)_30cm	0.070	0.1262	0.554	0.579

*Significant levels: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Table 4. Soil physical properties and soil microclimate factors explaining the burrows' portals orientation in the high plague frequency area

Variable	**Estimate**	**Std Error**	**t-value**	**Pr(>|t|)**
(Intercept)	3.393	1.126	3.012	0.00352**
Depth1 (0 - 30 cm)	-0.019	0.016	-1.229	0.22295
Depth2 (30 - 60 cm)	0.009	0.012	0.692	0.49101
Silt (%) (Ap)	-0.017	0.014	-1.213	0.22899
Clay (%) (Ap)	-0.017	0.020	-0.815	0.41783
Consistence Dry1 (0 - 30 cm)	0.514	0.289	1.778	0.07941
Consistence Dry2 (30 - 60 cm)	-0.418	0.292	-1.43	0.1568 .
Consistence Dry3 (> 60 cm)	-0.012	0.184	-0.065	0.94797
Infrared Temperature Celsius	-0.023	0.018	-1.281	0.20402

*Significant levels: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Table 5. Soil physical properties and soil microclimate factors explaining burrows' use in the high plague frequency landscapes

Soil properties	**Df**	**Deviance**	**Residual Df**	**Residual deviance**	**Pr(>Chi)**
Constant			45	63.77	
Depth1 (0 – 30 cm)	1	3.9567	44	59.813	0.04669 *
Depth3 (> 60 cm)	1	3.7019	43	56.111	0.05435.
Consistence Dry1 (0 - 30 cm)	1	1.5825	42	54.528	0.20841
Thermal Couple_10cm	1	4.509	41	50.019	0.03372 *

*Significant levels 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

3.3.5 Influence of soil physical properties and soil microclimate attributes on burrows' use in the medium plague area

Table 7 presents results showing that dry consistence of both topsoil and subsoil (ConsDry1-2) is statistically significant ($p<.05$) soil physical properties predicting burrow use. The signs for the coefficient in the dry consistence for the top and subsoils are positive and negative, respectively. This implies that extended use of burrow depends on the degree of resistance of burrow to collapse, a characteristic which is dependent on compaction or on the top-soil dry consistence where burrows are normally found. In the subsoil, dry consistence discourages burrowing into hard layers. This agrees with other studies that rodents avoid digging burrows in compacted areas to reduce energy use [19,47]. Other physical soil properties and soil microclimate attributes tested did not show any influence on burrow use, although the coefficients for soil depth (0 to >60 cm), textural particles and relative humidity seem to negatively influence rodent burrows' abundance.

3.3.6 Influence of soil physical properties and soil microclimate attributes on burrows' portals orientation in the medium plague frequency area

Table 8 presents results which depict that subsoil dry consistence, significantly ($p=.05$) influences negatively burrows' portals orientation. These results suggest that subsoil dry soil consistence discourages portal orientation, implying that the rodent portal set-up may not be influenced by the variables that were considered in the model.

Table 6. Influence of soil physical properties and soil microclimate attributes on rodent burrows' abundance in the medium plague frequency landscape

Variable	Estimate	Std error	z value	Pr(>|z|)
(Intercept)	353.11	29107.97	0.012	0.9903
Depth2 (30-60 cm)	-0.003	0.029	-0.095	0.9247
Depth3 (> 60 cm)	0.009	0.021	0.413	0.6799
Consistence dry1 (0-30 cm)	2.536	1.266	2.003	0.0452 *
Consistence dry2 (30-60 cm)	-2.821	1.344	-2.099	0.0358 *
Consistence dry3 (>60 cm)	0.786	0.801	0.982	0.3262
Infrared Temperature (Celsius)	-0.015	0.059	-0.247	0.8047
Thermal Couple_10cm	0.0121	0.036	0.335	0.7379
Relative humidity (%)_10cm	0.024	0.035	0.683	0.4947
Relative humidity (%)_30cm	-0.121	0.061	-1.991	0.0465 *

*Significant levels: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Table 7. Influence of soil physical properties and soil microclimate on burrows' use in the medium plague frequency area

Variable	Estimate	Std. error	t-value	Pr(>|t|)
Intercept	7.725873	8.100885	0.954	0.342
Depth1 (0-30 cm)	-0.0023	0.003197	-0.719	0.4732
Depth2 (30-60 cm)	-0.00261	0.002589	-1.008	0.3155
Depth3 (>60 cm)	-0.00014	0.002208	-0.065	0.9482
Sand % (Ap, 0-30 cm)	-0.06825	0.080756	-0.845	0.3996
Silt % (Ap, 0-30 cm)	-0.07055	0.081416	-0.866	0.3878
Clay % (Ap, 0-30 cm)	-0.07631	0.082167	-0.929	0.3548
Consistence Dry1 (0-30 cm)	0.232137	0.110805	2.095	0.0381 *
Consistence Dry2 (30-60 cm)	-0.23406	0.101675	-2.302	0.0229 *
Consistence Dry3 (>60 cm)	0.099652	0.090067	1.106	0.2706
Infrared temperature (C)	0.005249	0.006148	0.854	0.3948
Thermal Couple_10cm	0.0002948	0.003778	0.078	0.9379
Relative humidity (%)_10cm	-0.00028	0.004025	-0.071	0.9438
Relative humidity (%)_30cm)	-0.00475	0.003732	-1.272	0.2057

*Significant levels: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Table 8. Influence of soil physical properties and soil microclimate on burrows' portals orientation in the medium plague frequency area

	Estimate	Std. error	t-value	Pr(>|t|)
(Intercept)	2.496455	1.494738	1.67	0.0970
Silt (%) (Ap, 0 - 30 cm)	-0.00824	0.008869	-0.929	0.3544
Clay (%) (Ap, 0 - 30 cm)	-0.02037	0.01473	-1.383	0.1689
Consistence dry1 (0 - 30 cm)	0.596808	0.31892	1.871	0.0633 .
Consistence dry2 (30 - 60 cm)	-0.52158	0.22136	-2.356	0.0198 *
Consistence dry3 (>60 cm)	0.08976	0.155418	0.578	0.5645
Infrared tempera. (C	0.012672	0.017327	0.731	0.4657
Thermal Couple 10cm	0.003644	0.010816	0.337	0.7367
Relative humidity (%) 10cm	-0.00766	0.011076	-0.691	0.4904
Relative humidity (%) 30cm	-0.00844	0.010579	-0.798	0.4264

*Significant levels: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Although, the variables that were considered apparently did not show significant, the field data show that rodent burrows were oriented down the slopes or sideways in order to avoid surface run-off, or oriented in directions that avoid cold winds and/or that aid trapping of sunlight energy into the burrow. Our results are in agreement with those published earlier indicating that rodent orient burrows towards sunlight direction [19,20,53].

4. CONCLUSIONS AND RECOMMENDATIONS

4.1 Conclusions

<u>It is concluded from this study that</u>

There are differences of studied soil physical properties and soil microclimate in the studied landscape. The topsoil depth has influence on rodent burrows' abundance, where it was encouraging and discouraging burrowing in the high and medium plague frequency landscapes, respectively. It is also concluded that dry soil consistence (hardness) discourages rodent burrowing but encourages burrow use. In addition, relative humidity discourages burrowing in the medium plague landscape and due to fungal infection associated with high relative humidity it also seems to discourage flourishing of the plague vector (flea) larvae. The differences observed in soil physical properties and soil microclimate between the studied sites correspond with the observed rodent burrows' abundance in the two landscapes, implying that soil physical properties and soil microclimate could partly explain burrows' abundance in the area. This also partly explains the historical plague outbreak difference that exists between the two landscapes.

4.2 Recommendations

More research is strongly recommended on the role of soil physical and chemical properties and broad range of soil microclimate in influencing where burrows are set. This will add knowledge on the areas where rodent populations are likely going to be high, thereby facilitating forecasting, monitoring and management.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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