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SPECIAL ISSUE: AFRICAN SMALL MAMMALS

Factors influencing the distribution and abundance of small rodent pest species in agricultural landscapes in Eastern Uganda

Alex MAYAMBA[1,2,3*], Robert M. BYAMUNGU[2], Bram VANDEN BROECKE[4], Herwig LEIRS[4], Proches HIERONIMO[5], Alice NAKIYEMBA[1], Moses ISABIRYE[1], David KIFUMBA[1], Didas N. KIMARO[5], Mshaka E. MDANGI[6] and Loth S. MULUNGU[3]

[1] *Faculty of Natural Resources and Environment, Busitema University, Tororo, Uganda; e-mail: alexmayamba@gmail.com, alice.nakiyemba@gmail.com, isabiryemoseswb@gmail.com, kifumbadavidnsajju@gmail.com*

[2] *Department of Wildlife and Management, Sokoine University of Agriculture, Tanzania; e-mail: alexmayamba@gmail.com, robertbya@yahoo.com*

[3] *Pest Management Centre, Sokoine University of Agriculture, Morogoro, Tanzania; e-mail: alexmayamba@gmail.com, lothmulungu@yahoo.co.uk*

[4] *Evolutionary Ecology Group, University of Antwerp, 2610 Wilrijk, Belgium; e-mail: bram.vandenbroecke@uantwerpen.be, herwig.leirs@uantwerpen.be*

[5] *Department of Engineering Sciences and Technology, Sokoine University of Agriculture, Morogoro, Tanzania; e-mail: phmusigula@gmail.com, didasnahumu@gmail.com*

[6] *Department of Training, Extension services and Research, Ministry of Agriculture, Dodoma, Tanzania; e-mail: mesha78m@yahoo.com*

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Abstract. Small rodents are increasingly gaining importance as agricultural pests, with their distribution and abundance known to vary across landscapes. This study aimed at identifying ecological factors in the landscape that may influence small rodent distribution and abundance across agricultural landscapes in Uganda. This information may be used to inform the development of adaptive control measures for small rodent pests. Small rodent trapping surveys were conducted in three agro-ecosystem landscapes: Butaleja, Mayuge and Bulambuli districts in Eastern Uganda between November 2017 to June 2018 covering both dry and wet seasons. Data on small rodent abundance and richness, vegetation characteristics, land use/cover characteristics, farm management practices and soil characteristics were collected from quadrats. Additionally, Geographic Information System and remote sensing were used to determine vegetation characteristics (Normalized Difference Vegetation Index – NDVI) and land use/cover from satellite images. Our results showed that crop field state (including hygiene, crop type and growth stage) is the most important variable with an overall relative importance of 34.4% prediction value for the abundance of *Mastomys natalensis* across the landscape studied. In terms of number of species encountered (species richness), results showed field crop status scoring highest with an overall relative importance of 39.8% at predicting small rodent species richness. Second in importance for overall rodent abundance was percentage composition soil silt particles with 15.6% and 18.1% for species richness and abundance respectively. Our findings have important implications for small rodent management, where land use characteristics, especially field crop state, is a critical factor as different conditions tend to affect rodent abundances differently. The study thus recommends that control

* *Corresponding Author*

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efforts should be planned to consider field crop state; i.e. field hygiene where fields should be kept free of weeds to eliminate potential rodent breeding/habitation sites thus lowering rates of reproduction and population increase.

Key words: Boosted Regression Trees, NDVI, field crop status, landscape units

Introduction

Agriculture is the most dominant land use throughout much of Uganda. Sadly, this sector suffers from several production constraints such as droughts, low soil fertility, poor quality seeds, as well as pests and diseases. Pests and disease are key biotic factors limiting agricultural production in most rural farming communities in the country, resulting in chronic food insecurity (Oerke 2006). Among the different pests, rodents are responsible for a significant amount of pre- and post-harvest losses particularly to cereal crops in Uganda and the rest of East African region (Leirs et al. 1997, Makundi et al. 2006, Mulungu et al. 2010, Mayamba et al. 2019). Their distribution and abundance have been shown to vary temporally and spatially due to different ecological factors including land use/land cover types (Fraschina et al. 2014, Hieronimo et al. 2014), soil properties (Massawe et al. 2008, Meliyo et al. 2015) climate (Leirs et al. 1997), and land management practices (Massawe et al. 2007, Hieronimo et al. 2014). For instance, the Normalized Difference Vegetation Index (NDVI), a remote sensing based proxy indicating the greenness of the vegetation in an area, has been demonstrated to be the most important predictor of small rodent species richness and abundance in a semi-arid climate in Tanzania (Chidodo 2017). Other earlier reports have demonstrated that rainfall is the most important predictor of population abundance particularly for *Mastomys natalensis* in a bimodal climate (two rainfall seasons/year) in Tanzania (Leirs et al. 1997). Soil types have also been shown to influence rodent abundance with sandy loam soils sustaining higher rodent abundance compared to clay soils (Meliyo et al. 2015, Mlyashimbi et al. 2019).

Current control efforts are predominantly reactive and aim at killing (Mulungu et al. 2010, Krijger et al. 2017), via the use of different chemicals (rodenticides), which are relatively expensive for the peasant farmers, affect non target organisms and are often followed by recolonization shortly after treatment (Stenseth et al. 2001, 2003, Singleton et al. 2007, Mulungu et al. 2010). More effective rodent control measures based on ecological information are therefore needed (Mulungu 2017, Swanepoel et al. 2017). There is need for a detailed understanding of the landscape ecological factors that influence rodent abundance in order to better plan appropriate management strategies. For example some landscapes have been suggested to be less prone to pest infestation than others (Parry & Schellhorn 2013) and the ecological factors involved need to be identified.

Agricultural land use is another important attribute affecting rodent abundance. Indeed, the intensification of agriculture tends to favour more generalist species compared to habitat-specialist species which prefer low intensity farmed land (Mill et al. 2003, Butet et al. 2006, Fraschina et al. 2014). Additionally, the use of machinery, introduction of new crops, changing agronomic practices (Robinson & Sutherland 2002, Massawe et al. 2007) and the growing use of chemicals such as fertilizers and pesticides are reported to influence the dynamics of biodiversity in agricultural land (Mclaughlin & Mineau 1995, Stoate et al. 2001).

Unfortunately, despite the importance of rodent damage in agricultural land knowledge of the key factors influencing rodent distribution and abundance is still minimal in Uganda (Mayamba et al. 2019). Available studies in Uganda focus on rodents in national parks and natural forest (Southern 1962, Delany 1971, Isabirye-Basuta & Kasenene 1987, Clausnitzer & Kityo 2001, Ssuuna et al. 2020). Most studies of rodent abundance in agricultural land have been conducted in Tanzania (Hieronimo et al. 2014, Swanepoel et al. 2017, Chidodo et al. 2020). However, caution should be exercised in extrapolating these findings to other regions with different environments and farming systems. For example, the application of NDVI reported as the most important predictor variable of rodent abundance in a bimodal semi-arid region in Tanzania (Chidodo 2017, Chidodo et al. 2020) could be different in a semi-arid area with a unimodal rainfall pattern. It is therefore important to study key ecological factors that shape rodent species abundance in any given locality in order to design effective management plans.

This study set out to understand and document important landscape factors (e.g. land use/cover, terrain characteristics, soil physical properties and rainfall) that

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influence small rodent species richness and abundance across different agroecosystem landscapes in Eastern Uganda. The information is expected to be utilized in developing more robust temporal and spatial probabilistic models for predicting potential rodent pest outbreaks in the country.

Material and Methods

Description of study site

The study was conducted in three districts in Eastern Uganda with contrasting agro-ecosystems; (i) Kigulu parish in Mayuge district, (06°16′ S, 37°31′ E), in a mid-altitude zone (approximately 1,100 m a.s.l.), which is characterized of mixed crops with maize as a major seasonal food and cash crop. (ii) Kapisa parish in Butaleja district, (00°57′ N, 34°44′ E), which is a mid-low altitude zone (approximately 1,050 m a.s.l.), characterized by several swamps and low-lying areas which are supplied with water from the River Manafa. These low lying areas are utilized for growing lowland rice as a major cash crop for many of the households in the district. Other crops include maize, sorghum, cassava, sweet potato beans, (iii) Bukhalo parish in Bulambuli district: the area lies at 01°18′ N, 34°15′ E at the foot of Mount Egon at approximately 1,160 m a.s.l. The area is mainly characterized by small to medium scale maize farming, although cotton is grown during some seasons as a cash crop. A map of the location of the study sites is shown in Fig. 1 and a detailed description of each of the studied sites is given in Table 1.

Acquisition of remote sensing data

Multi temporal Landsat 8 (Operational Land Imager – OLI) images were obtained to map landscape characteristics including land use/land cover types for different periods in the dry and wet seasons (Tables 2, 3). All the images used were already orthorectified, terrain corrected and georeferenced. The high-resolution Google Earth satellite images were used for interpretation of Land Use and Land Cover (LULC) types to develop training data sets for supervised classification of vegetation characteristics.

Mapping of vegetation characteristics

Remote sensing, Geographic Information System (GIS) and field surveys were used to map vegetation characteristics (Weih & Riggan 2010, Ralaizafisoloarivony et al. 2014). Vegetation characteristics (NDVI), land use types (land management practices, crop type, garden status and

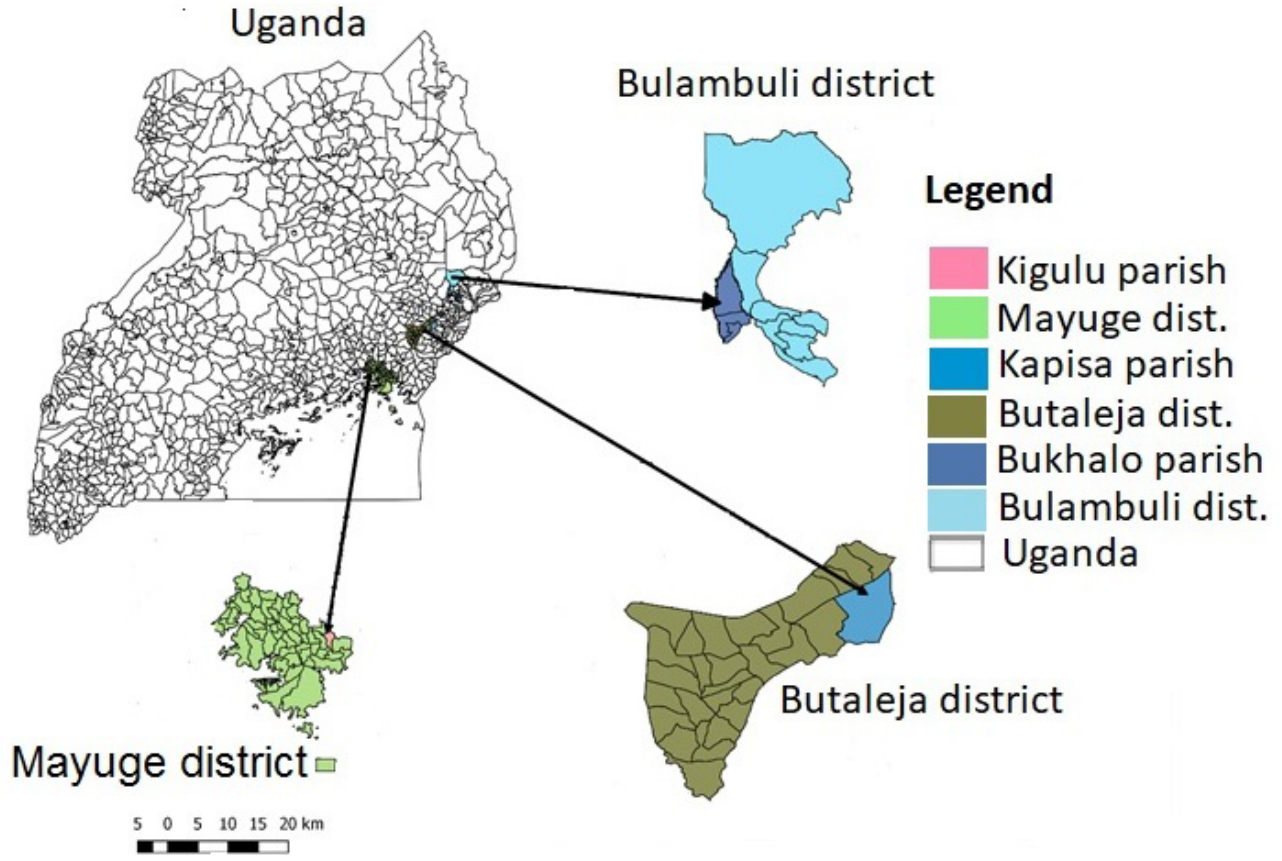


Fig. 1. Map showing the study sites.

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Table 1. Detailed description of landscape characteristics of the studied landscape units.

Landscape units	Landscape characteristics
Kigulu parish, Kigandalo subcounty Mayuge district	- Mixed cropping system (maize, sweet potato, beans, sugarcanes) - Medium altitude - Two distinct rainy seasons per year - Crop production characterized by small fragmented plots ranging from less than an acre to about five acres - Crop cultivation plots are intermingled with temporary fallow lands which contain shrub trees and short thickets - Land clearing is by both hand hoe and oxen plough - Complex of undulating and rocky hills - Soil type; black and grey non cracking clays often calcareous with moderate drainage - AO soil class; gleysols
Kapisa parish, Kapisa subcounty, Butaleja district	- Characterized by low-lying wetland patches - Mid to lowland altitude - Lowland rice crop mainly grown in the wetland patches - Crop cultivation plots are intermingled with temporary fallow lands which contain shrub trees and short thickets - Land clearing is dominantly done by hand hoe - Soil type; greyish and yellowish-brown sands and sand clays with moderate to excessive drainage - FAO soil class; gleysols or petric plinthosols
Bukhalo parish, Bukhalo subcounty, Bulambuli district	- Foot hills of Mount Elgon - Medium to high altitude - Land clearing mainly by tractor ploughing - Maize fields on about 1 ha and above - Crop cultivation plots are intermingled with temporary fallow lands which contain shrub trees and short thickets - Sometimes practice relay cropping - Soil type; dark brown clays and clay loams with moderate drainage - FAO soil class; vertisols or luvisols

Table 2. Temporal characteristics of Landsat 8 (Operational Land Imager – OLI) data acquisition.

District	Season	Required period	Landsat 8 (OLI 30 m) date
Mayuge	Dry 1	Dec, Jan and Feb	7/Feb/2018
	Wet 1	Mar, Apr and May	3/Apr/2018
	Dry 2	June and July	17/Jul/2018
	Wet 2	Sept, Oct and Nov	21/Nov/2017
Butaleja	Dry 1	Dec, Jan and Feb	15/Jan/2018
	Wet 1	Mar, Apr and May	27/Apr/2018
	Dry 2	June and July	21/Jul/2018
	Wet 2	Sept, Oct and Nov	21/Nov/2017
Bulambuli	Dry 1	Dec, Jan and Feb	15/Jan/2018
	Wet 1	Mar, Apr and May	27/Apr/2018
	Dry 2	June and July	21/Jul/2018
	Wet 2	Sept, Oct and Nov	21/Nov/2017

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Table 3. Micro land use/landcover classes.

Micro Class	Description
Human settlement	Man-made structures, e.g. buildings
Agriculture	Cultivated areas
Dense vegetation	Forested areas
Dry farmlands	Crops at dry harvest stages
Shrubs	Short thickets
Open fields	Cleared land for planting, without crop or vegetation

crop field status; a descriptive factor including field hygiene, crop type and growth stage) were described and estimated using square quadrats (100 × 100 m) placed randomly in each of the sub counties in the studied districts. Spatial location of the vegetation types was recorded using an Etrex 10 Garmin Global Positioning System (GPS) receiver with accuracy of less than 5 m. The Land Cover Classification System (LCCS) and Earth Cover Classification System (ECCS) guidelines from the Food and Agriculture Organization (FAO) and Open Foris Initiative (OFI) respectively, were used to identify vegetation types, from which general vegetation classes were generated (Di Gregorio & Jansen 2005).

Generation of general land cover and land use types

The Landsat 8 (OLI) images obtained from the United States Geological Survey (USGS) at different seasonal periods, as described in Table 2, were used

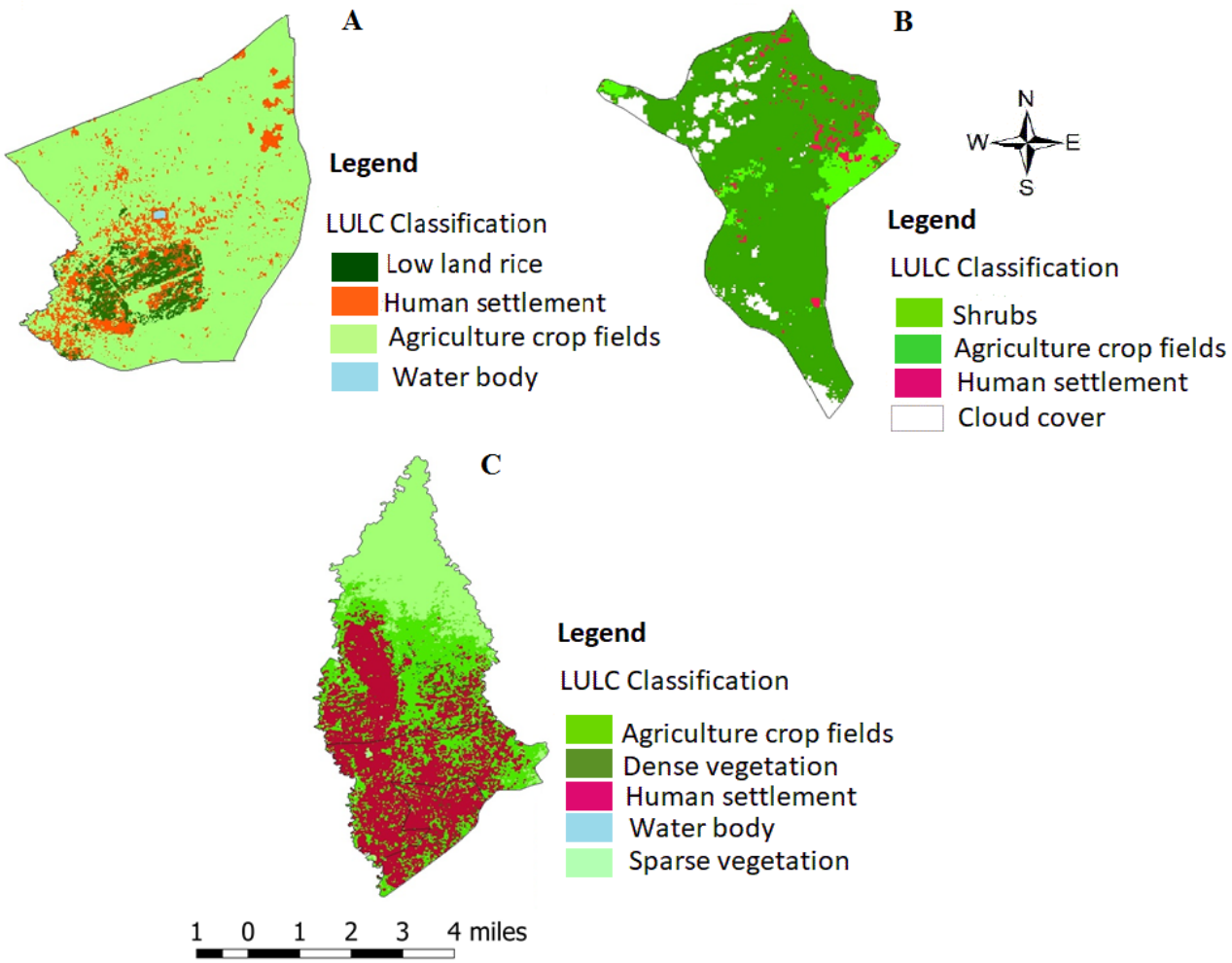


Fig. 2. Land use/land cover (LULC) map representative of A) Kapisa parish, Bualeja district, B) Kigulu parish, Mayuge district and C) Bukhalo parish, Bulambuli district.

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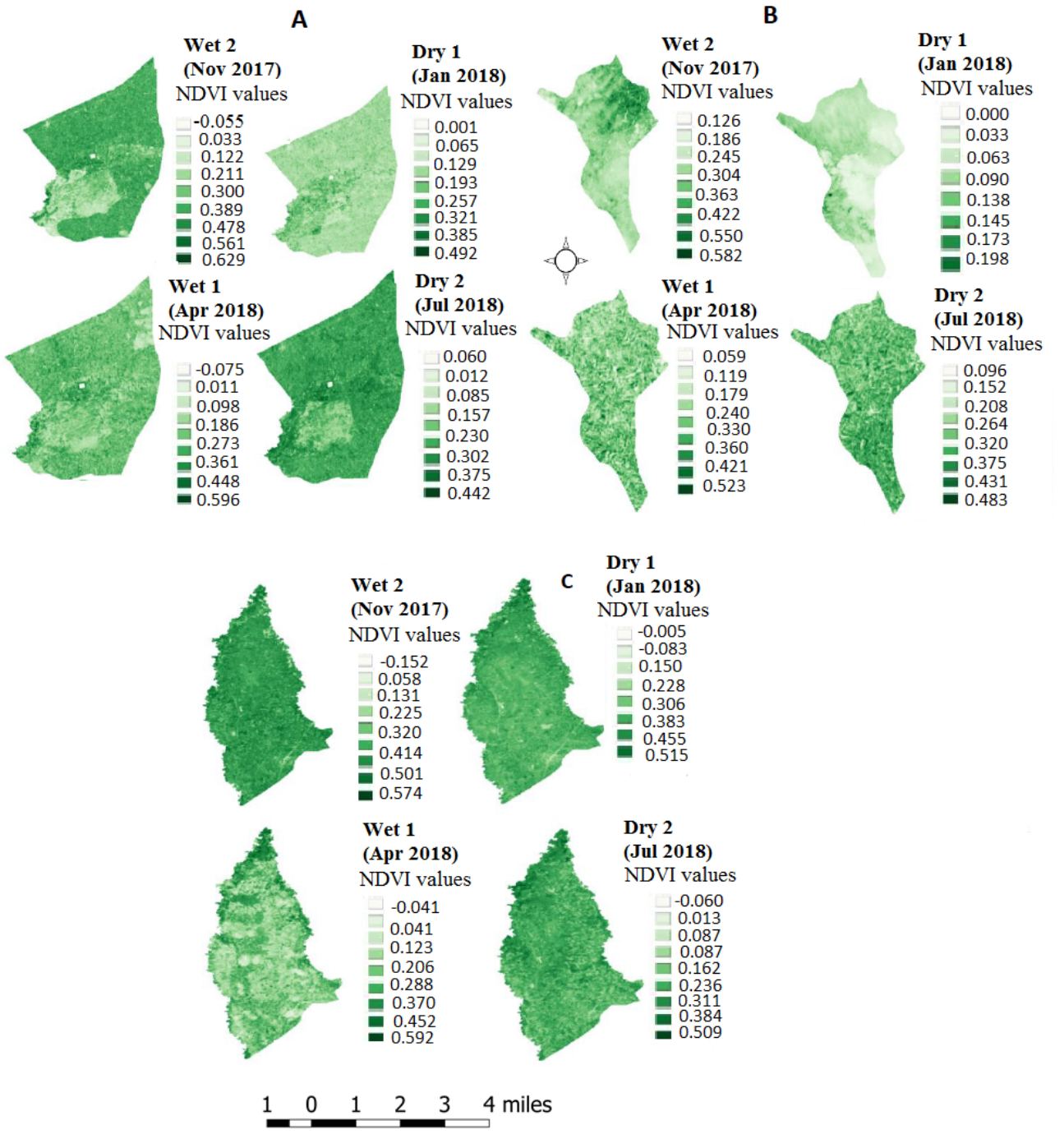


Fig. 3. Normalized Difference Vegetation Index (NDVI) maps covering the different seasons across the three study sites: A) Kapisa parish in Butaleja district, B) Kigulu parish in Mayuge district and C) Bukhalo parish in Bulambuli district.

for mapping land use/land cover types as described by a set of attributes for each studied site (Table 1). Spatial referenced field data allowed us to define characteristic tone, texture and patterns of land use/cover classes on the display of the Landsat 8 (OLI) colour composite image (Hieronimo et al. 2014).

Cluster pixels in Landsat 8 (OLI) satellite images were categorized into six classes using supervised classification procedure: agriculture, settlement, dry farmlands, dense vegetation, open fields and shrubs. To obtain these classes, a Region of Interest (ROI) was defined for each of the land cover classes in the output image. Maximum likelihood classification was performed to assign each pixel in the image to the class that has the highest probability of obtaining land use/cover maps for each studied landscape site at a spatial resolution of 30 × 30 m. Sample data sets created for each vegetation class were used for categorization of the spectral classes into general vegetation classes (land use/lad cover classes) in ArcMap 10.1 and Semi-Automatic Classification Plugin (SCP) in the QGIS software (Fig. 2).

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These features were described at micro spatial scales to obtain sample data sets for classification of the image into land use/land cover attributes at landscape unit level (Table 3) used for predicting spatial and temporal small rodent's richness and abundance.

Determination of NDVI across vegetation habitats

NDVI was determined from Landsat 8 (OLI) satellite images covering the periods corresponding with the rainfall patterns as described in Table 2. It was calculated as the normalized difference in reflectance band between the red (0.636-0.673 μm) and Near Infra-Red (NIR, 0.851-0879 μm) electromagnetic spectrum using equation 1 (Pettorelli et al. 2011).

(eq. 1)

$$NDVI = \frac{NIR - R}{NIR + R}$$

Where NDVI = Normalized Difference Vegetation Index, R = surface reflectance in the red portion of the electromagnetic spectrum, NIR = reflectance in the Near Infra-Red band of the electromagnetic spectrum.

To eliminate the effect of clouds, the Maximum Value Composite (MVC) algorithm in QGIS was used during NDVI data processing. In the MVC procedure, the multi-temporal geo-referenced NDVI data were evaluated on a pixel basis, to retain the highest NDVI value for each pixel location. The raster calculator tool in QGIS was used to generate the NDVI maps for the different study sites across sampling seasons (Fig. 2A-C). Further extraction of NDVI values for each trapping field was done using the identifier tool where five NDVI value points were randomly selected around the field coordinate points and an average generated as a representative NDVI value for that field (Fig. 3). This was done for all the trapping fields.

Ground truthing and field characterization

Based on logistics, 20 quadrats (100 × 100 m) in each parish in the respective district were randomly selected using a randomization tool in QGIS, with a buffer zone around main roads and setting a minimum separation distance of 500 m from each quadrat. A total of 60 quadrats were therefore geographically located for ground truthing and detailed spatial landscape vegetation characteristics were collected such as type of crop present in the field, the field hygiene (weedy or clean), stage of crop development (vegetative, mature stage, dry harvest stage) and soil physical characteristics (silt sand and clay particle composition).

Small rodent trapping

Trapping of small rodent animals was conducted following the procedure by Aplin et al. (2003) using Sherman live traps (H.B. Sherman Traps, Inc., Tallahassee, FL, USA). In each of the 60 geo-referenced quadrats, 49 Sherman live traps were set in a 60 × 60 m configuration (seven trapping lines each with seven trapping stations, 10 m apart) were used as these were shown to provide substantial data for rodent Cardiac Magnetic Resonance (CMR) studies (Aplin et al. 2003). Traps were baited with peanut butter and maize flour and were inspected for two trap nights at each quadrat. Trapping commenced in Wet season 2 (November 2017), Dry season 1 (Jan-Feb 2018), Wet season 1 (March/April 2018) and ceased in Dry season 2 (July 2018). The nomenclature by Wilson & Reeder (2005) was used as the main reference to identify the rodent species captured in the study areas and later cross referenced with Happold (2013). The community structure in this study was described as relative composition based on the trappable rodent species in the study sites.

Rainfall data acquisition

Data for daily precipitation for the months of data collection was obtained from the Uganda National Meteorological Authority for the three different studied landscape units (Butaleja, Mayuge and Bulambuli districts). Data were summarized into total monthly precipitation and monthly rainy days; these were considered as predictor variables for small rodent abundance and richness, and were subjected to Boosted Regression Tree (BRT) analysis.

Data analysis

Data on small rodent species recovered from the 20 trapping grids in each district were pooled to obtain total small rodent species composition per landscape unit.

Boosted Regression Tree modelling

BRT modelling was used to establish the relationships between landscape ecological factors and small rodent abundance and species richness across the studied landscapes. Landscape ecological factors were used as predictor variables and they included; mean NDVI, percentage cover of farm land, settlement, shrubs, dense vegetation, sparse vegetation, farm management practices

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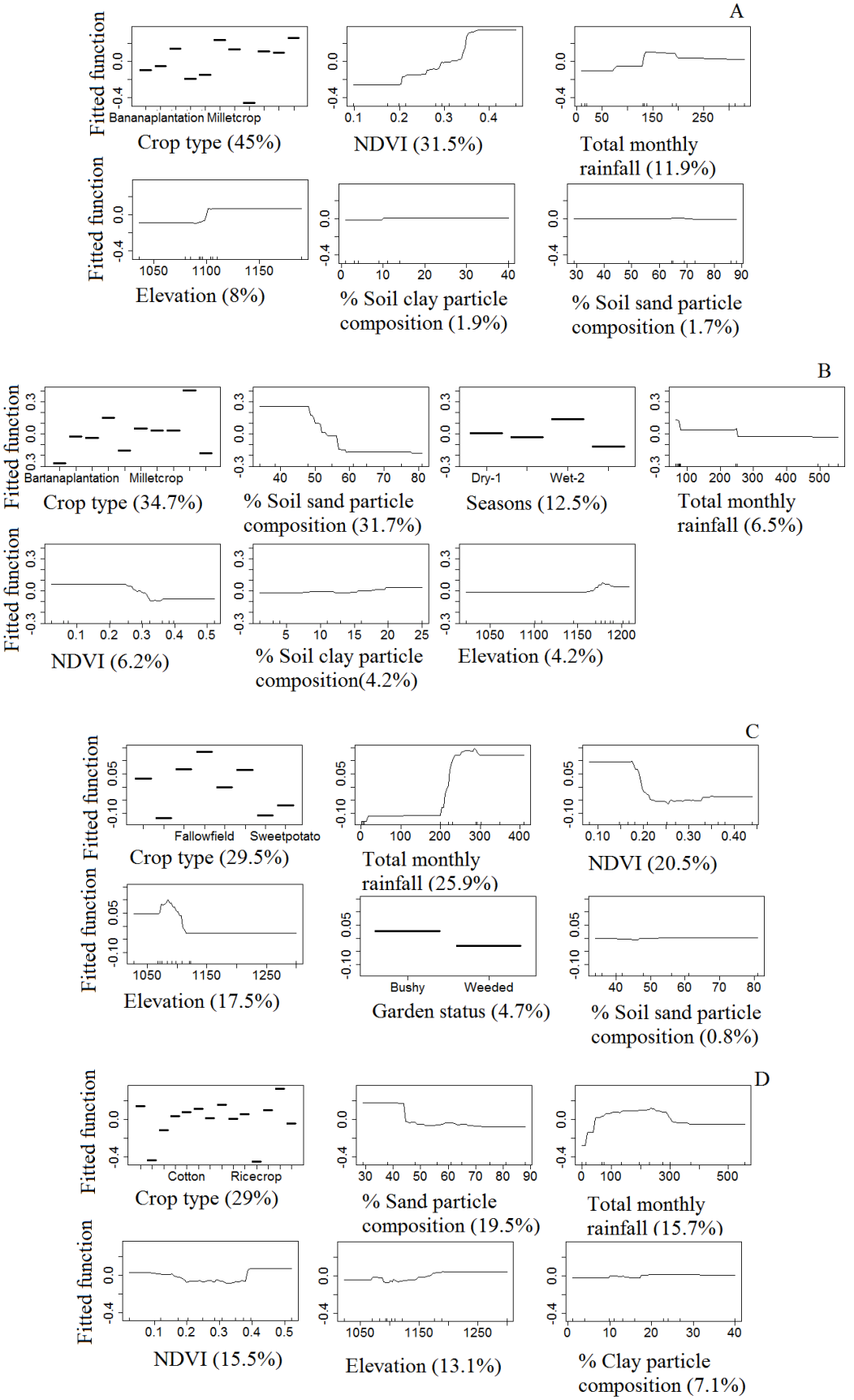


Fig. 4. Partial dependence plots showing the relationships/effects of predictor variables with *M. natalensis* population abundance. A) Butaleja, B) Mayuge districts, C) Bulambuli district and D) overall (combined for the three districts). The relative importance of each variable is indicated in brackets. CV deviance = 3.88, SE = 0.71, number of trees = 3,200; CV deviance = 7.104, SE = 1.781, number of trees 2,950; CV deviance = 4.092, SE = 0.442, number of trees = 2,500 and CV deviance = 5.281, SE = 0.74, number of trees 1,800 for Butaleja, Mayuge, Bulambuli and overall (combined data) respectively. Key: CV = Cross-Validation, SE = Standard Error, NDVI = Normalized Difference Vegetation Index.

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Table 4. Species composition of small rodents recovered in the trapping survey conducted in Mayuge, Butalejja and Bulambuli districts during the study period. Values in brackets () show percentage composition.

Species	Number of animals in Bulambuli	Number of animals in Butaleja	Number of animals in Mayuge	Total number of animals
Mastomys natalensis	346 (72.4)	298 (60.5)	492 (67.3)	1136 (66.7)
Lemniscomys zebra	28 (5.9)	114 (23.1)	28 (3.8)	170 (10)
Mus triton	45 (9.4)	43 (8.7)	115(15.6)	203 (11.9)
Aethomys hindei	35 (7.3)	13 (2.6)	55 (7.5)	103 (6.0)
Lophuromys sikapusi	1 (0.2)	2 (0.4)	19 (2.6)	22 (1.3)
Arvicanthis niloticus	19 (4)	19 (3.9)	8 (1.1)	46 (2.7)
Thallomys paedulcus	0 (0)	2 (0.4)	0 (0.0)	2 (0.1)
Graphiurus murinus	2 (0.4)	0 (0.0)	11(1.5)	13 (0.8)
Steatomys parvus	0 (0.0)	0 (0.0)	2 (0.3)	2 (0.1)
Gerbilliscus kempi	0 (0.0)	1 (0.2)	0 (0.0)	1 (0.1)
Dasymys incomtus	0 (0.0)	0 (0.0)	1(0.1)	1 (0.1)
Rattus rattus	2 (0.4)	0 (0.0)	0 (0.0)	2 (0.1)
Grammomys gazellae	0 (0.0)	1 (0.2)	1(0.1)	2 (0.1)
Oenomys hypoxanthus	0 (0.0)	0 (0.0)	1(0.1)	1 (0.1)
Total	478	493	733	1704
Number of species	8	9	11	14
Simpson Diversity Index	0.551	0.655	0.5788	
Chao-1	8	10	13	

(crop type, garden status and field crop status), soil physical characteristics (silt, sand and clay particle percent composition), rainfall (rainy days and total monthly rainfall, rainfall seasons), and elevation. Rodent abundance and species richness were the response variables. The analysis was performed separately for each landscape unit and finally pooled to generate the overall influence of predictor variables across the studied landscape units. BRT models were constructed in R statistical program version 3.5.8 (R Development Core Team 2006) using custom code (Elith et al. 2008). Analyses were based on a Poisson distribution. The 10-fold Cross-Validation (CV) was used for model development and validation, with the benefit of still using the full data set to fit the final model. Models were fitted using the gbm.step function following selection of appropriate settings for learning rate (0.01-0.0001) and bag fraction (0.5-0.75) as found by repeated trial-and-error. Tree complexity i.e. the number of nodes in a tree, was set to five, according to recommendations by Elith et al. (2008) for small datasets. The measure of model performance was CV deviance and standard error (Elith et al. 2008, Williams et al. 2010). The combination of learning rate and bag fraction settings with the lowest CV deviance and standard error was the one selected to produce the final BRT model (Williams et al. 2010). Also, during data exploration all predictor variables were tested for ecologically acceptable levels of collinearity (i.e. individual Variance Inflation Factor (VIF) of < 5, Zuur et al. 2010, Aertsen et al. 2012). Partial dependency plots were used for interpretation and to quantify the relationship between each predictor variable and small rodent abundance and richness (Elith et al. 2008).

Where the most important predictor variable was categorical, a one-way ANOVA was performed to establish the significant effects between species richness and abundance with the predictor variables (XLSTAT 2017). The data was first tested for normality and where necessary log 10 transformations were conducted to meet the assumptions of ANOVA. Further, where significant effects where obtained the post hoc

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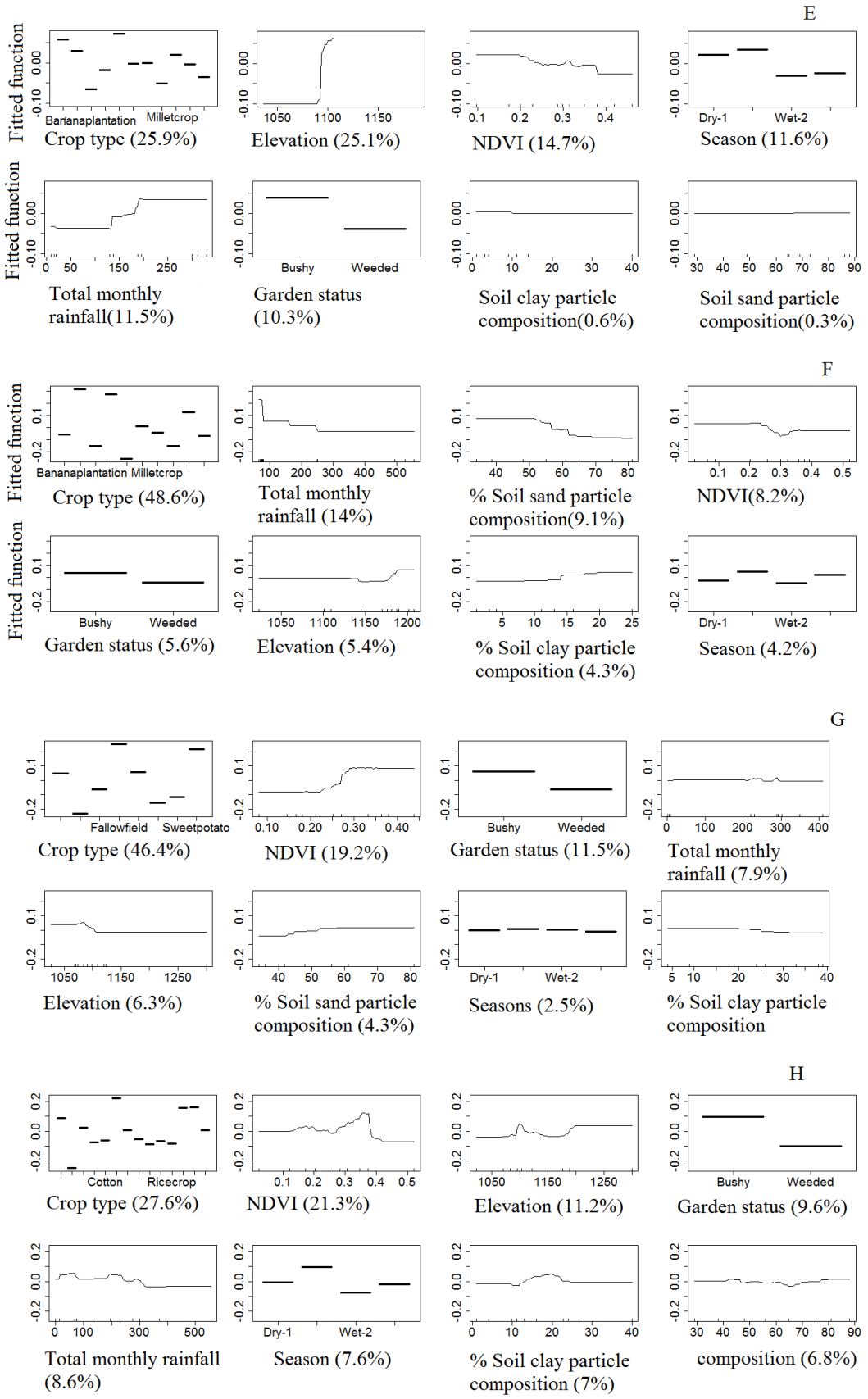


Fig. 5. Partial dependence plots showing the relationships/effects of predictor variables with small rodent species richness. E) Butaleja, F) Mayuge districts, G) Bulambuli and H) overall (combined data for three districts). The relative importance of each variable is indicated in brackets. CV deviance = 0.55, SE = 0.04, number of trees = 1,500; CV deviance = 0.69, SE = 0.11, number of trees 4,500; CV deviance = 0.41, SE = 0.04, number of trees = 3,500 and CV deviance = 0.56, SE = 0.03, number of trees 2,800 for Butaleja, Mayuge, Bulambuli and overall (combined districts) respectively. Key: CV = Cross-Validation, SE = Standard Error, NDVI = Normalized Difference Vegetation Index.

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mean separation using Tukey's Honest Significant Difference (HSD) test was performed.

Results

Small rodent species richness and abundance

The study yielded 21,168 trap nights with 478, 493 and 733 small rodent individuals trapped in Bulambuli, Butaleja and Mayuge district landscape units respectively. These comprised of 14 small rodent species with the multimammate rat (*Mastomys natalensis)* being the most abundant rodent species with a total of 1,136 (66.7%) individuals across the three landscape units. There were a number of species that were rarely recorded in the study, with less than five individuals trapped during the whole study period. These included; *Gerbilliscus kempi*, *Grammomys gazellae*, *Dasmys incomtus*, *Oenomys hypoxanthus*, *Rattus rattus*, *Thallomys paedulcus* and *Steatomys parvus*. The results also showed that species richness was higher in Mayuge landscape unit (11 species) compared to Butaleja (nine species) and Bulambuli (eight species) (Table 4). Influence of landscape ecological factors on small rodent (*M. natalensis*) abundance.

Vegetation characteristics

NDVI was the only vegetation attribute considered in the model. There was variation in the model strength of NDVI as a predictor of *M. natalensis* population abundance. NDVI was the second most important predictor overall with 21.3% relative influence. In Butaleja it also ranked second with relatively higher influence (31.5%). In Bulambuli it ranked third with 20.5% influence whereas in Mayuge it ranked fifth with low influence (6.2%). The dependence plots in Butaleja showed higher *M. natalensis* abundance with increase in NDVI up to an index of 0.4 (Fig. 4).

Land use/land cover

This included both land use/cover classes and farm management practices. The important variable here was crop type which ranked the most important predictor variable in the model for predicting *M. natalensis* population abundance both in individual study sites and overall (Fig. 4). The Kruskal-Wallis test of the overall effect of crop type on *M. natalensis* abundance was significant ($\chi^2 = 27.3$, df = 13, $p = 0.0114$), with highest abundance in sugarcane (11 ± 7 animals/0.5 ha), followed by maize intercropped with beans (6 ± 6 animals/0.5ha) and sorghum (6 ± 5 animals/0.5ha) (Table 5). Significantly lowest abundances were recorded in banana plantations (0 animals/0.5 ha). The separate site analysis on the effect of crop type showed no significant differences (Table 5).

Soil physical characteristics

The percentage composition of silt, sand and clay particles in the soil was considered in the model. The overall ranking showed sand to be

Table 5. Median (±SD) population abundance of *Mastomys natalensis* in the different crop types in Mayuge, Butaleja, Bulambuli district and overall. Mean values followed by same letters are not significantly different from each other. Columns with values not followed by letters indicate no significant difference.

Crop type	Overall	Bulambuli	Butaleja	Mayuge
Banana plantation field	0 ± 3^{e}	0 ± 4	1 ± 0	1 ± 1
Fallow field	5 ± 9^{ab}	5 ± 6	2 ± 5	5 ± 5
Sweet potato field	4 ± 4^{cd}	4 ± 3	8 ± 4	2 ± 4
Maize bean Intercrop	6 ± 6^{b}	8 ± 4	7 ± 6	6 ± 9
Maize monocrop field	5 ± 4^{cd}	5 ± 4	4 ± 5	6 ± 4
Mixed cropping	4 ± 7^{cd}	2 ± 3		5 ± 8
Cassava plantation field	3 ± 4^{cd}	7 ± 8	4 ± 3	3 ± 0
Rice crop	1 ± 2^{d}		1 ± 2	
Cotton Field	6 ± 3^{bc}		6 ± 3	
Millet crop	3 ± 7^{bc}		8 ± 9	3 ± 0
Sorghum crop	6 ± 5^{bc}		6 ± 5	
Sugarcane field	11 ± 7^{a}		5 ± 0	12 ± 6
Coffee plantation	4 ± 7^{bc}			4 ± 7
χ^2	27.3	10.3	16	11.8
df	12	6	10	9

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Table 6. Median (±SD) population abundance of *Mastomys natalensis* in the different crop type fields in Mayuge, Butaleja, Bulambuli district and overall. Mean values followed by the same letters are not significantly different from each other. Columns with values not followed by letters indicate no significant difference.

Crop type	Overall	Bulambuli	Butaleja	Mayuge
Banana plantation field	2 ± 1^{b}	1 ± 0^{c}	3 ± 0	2 ± 1^{bc}
Fallow field	3 ± 2^{ab}	4 ± 1^{a}	3 ± 1	4 ± 2^{a}
Sweet potato field	3 ± 1^{ab}	3 ± 1^{ab}	3 ± 1	2 ± 1^{ab}
Maize bean Intercrop	2 ± 1^{b}	2 ± 1^{b}	4 ± 1	3 ± 1^{ab}
Maize monocrop field	3 ± 1^{ab}	3 ± 1^{ab}	3 ± 1	2 ± 1^{bc}
Mixed cropping	2 ± 1^{b}	2 ± 1^{b}		2 ± 1^{bc}
Cassava plantation field	3 ± 1^{ab}	2 ± 1^{b}	3 ± 1	4 ± 0^{ab}
Rice crop	2 ± 1^{b}		2 ± 1	
Cotton Field	2 ± 1^{b}		2 ± 1	
Millet crop	1 ± 1^{c}		2 ± 1	1 ± 0^{c}
Sorghum crop	4 ± 2^{a}		4 ± 2	
Sugarcane field	3 ± 1^{ab}		2	3 ± 1^{ab}
Coffee plantation	1 ± 1			1 ± 1^{c}
$\chi 2$	26.75	23.68	8.65	18.52
df	12	6	10	9
p-value	0.013	0.001	0.566	0.029

the third most important predictor variable with 19.5% relative importance. The dependence plots showed higher abundances of *M. natalensis* when percentage composition of sand ranged between 30-40% and a decline above 50%. Independent site modelling showed percentage composition of sand ranking second with 31.7% relative influence in Butaleja while in the other sites soil composition ranked very low (Fig. 4A-D).

Climatic variables

Rainfall was the only climatic variable considered for modelling *M. natalensis* abundance. Total monthly rainfall in the month prior to trapping and number of rainy days were the two parameters used for model prediction. The highest ranking of rainfall was observed in Bulambuli district, where it came second with 25.9% relative influence while ranking fourth overall. The dependence plots showed a high positive relationship with *M. natalensis* abundance when rainfall exceeded 200 mm in Bulambuli district. In Mayuge and Butaleja, rainfall in the month prior to trapping showed low influence (Fig. 4A-D). Rainy days ranked very low with very low percent relative influence and thus the factor was dropped during modelling.

Other predictor variables included elevation (altitude) which ranked third in importance in Bulambuli with 17.5% relative influence and fifth overall with 13.1%. The dependence plots generally showed higher abundances at high elevation.

Influence of landscape ecological factors on small rodent species richness, vegetation characteristics

Here NDVI was second most important predictor overall with 21.3% relative influence on prediction of species richness. NDVI ranked second in Bulambuli with 19.2%, third in Butaleja and fourth in Mayuge. The dependence plots for overall ranking and Bulambuli showed higher species richness with an increase in NDVI index up to 0.4 and a decline above 0.5 (Fig. 5E-H).

Land use/land cover characteristics

As for abundance, crop type ranked the most important predictor variable for species richness overall and in each district independently. The highest relative influence was observed in Mayuge with 48.6% relative influence (Fig. 5F). The Kruskal-Wallis analysis of the effect of crop type on species richness showed significantly higher richness in sugarcane overall (4 ± 2 species/0.5 ha) and in fallow fields for Bulambuli (4 ± 1 species/0.5 ha) and Mayuge (4 ± 2 species/0.5 ha) (Table 6). Significantly low richness was observed in coffee and millet (Table 6).

Climatic influence

Generally, total monthly rainfall in the month prior to trapping ranked low overall and for individual

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districts, ranking second in Mayuge with low relative influence of 14% (Fig. 5). The dependence plots of the showed a negative relationship between species richness and total monthly rainfall above 200 mm. Number of rainy days was shown to have had very minimal influence on species richness and was omitted during modelling.

Soil physical characteristics

The role of soil physical characteristics seemed to have a very low influence on species richness with percentage composition of sand ranking third in Mayuge with 9.1% relative influence (Fig. 5). Elevation was the other landscape ecological variable considered and it ranked second in Butaleja with 25.1% and third overall with 11.2% relative influence. The dependence plots in Butaleja showed higher richness at elevations above 1,100 m a.s.l.

Discussion

Small rodent species richness

In the present study, 14 species of small mammals were found across the three studied landscapes in Eastern Uganda, with *M. natalensis* being the most dominant species. These results are in line with previous studies performed in most parts of the sub-Saharan African that have reported a similar number of small rodent species inhabiting agricultural landscapes, with *M. natalensis* being the most dominant species (Makundi et al. 2007, Massawe et al. 2012, Mulungu 2017, Mayamba et al. 2019). This is important in light of pest damage, since *M. natalensis* is the most important agricultural rodent pest species in Eastern and Southern Africa, responsible for substantial damage to crops in agricultural landscapes (Leirs et al. 1997, Makundi et al. 1999, Mwanjabe et al. 2002, Taylor et al. 2012, Swanepoel et al. 2017).

Our models showed that the influence of landscape ecological factors was variable with land use characteristic variables being more important than the others in predicting small rodent species richness. Specifically, crop type ranked the most important predictor variable. Sugarcane, fallow fields, sorghum and maize intercropped with beans showed relatively higher richness compared to other crops. It is possible that these fields are more heterogenous (complex) thus offering a greater variety of habitats which can support different species. Indeed, earlier reports such as that of Silva et al. (2005), showed that the structural complexity of landscapes, as measured by coverage and shape of residual forest patches, positively correlated with greater species richness, their explanation being that complex habitats exhibit micro habitats which offer diverse resources for several rodent species. Other studies have also demonstrated higher rodent species richness in agricultural fields with well-developed vegetation cover and with less disturbance (Fischer et al. 2011, Fischer & Schröder 2014). Additionally, these fields usually exhibit low human interaction/disturbance and thus are relatively stable agricultural environments, another factor which may explain the higher richness (Hieronimo et al. 2014). Generally the study found a relatively low species richness across the sites and overall, a result that is supported by previous studies that small mammal assemblages inhabiting agro-ecosystems tend to be dominated by only a few species (Stefania et al. 2014).

NDVI, a vegetation characteristic index was also important in predicting species richness across the different study landscapes. Its influence is similar to crop type and could be associated with food availability and suitable habitat provided by green vegetation. Similar earlier findings have shown higher small mammal richness in areas with higher NDVI index values (Chidodo 2017).

Small rodent abundance

The relative abundances of small rodent species associated with agriculture fields is critical as the numbers often result in crop damage (Fidler 1994, Mwanjabe et al. 2002, Mulungu 2017). In modelling we only considered the most abundant species *M. natalensis*, the key pest in the region. Our models showed that land use characteristics, specifically, crop type is the most important predictor for small rodent abundance in the studied area. We attribute our results to two key components: food (both quality and quantity) and suitable habitats in terms of ground cover. The latter provides the animals with more shelter which may reduce predation risk and thus increase survival and abundance (Kotler 1984, Adler 1995, Shanker 2001, Jacob 2003, Massawe et al. 2007, Gheler-Costa et al. 2012, Guidobono et al. 2018).

We found higher population abundances of *M. natalensis* in fields with sugarcane, maize intercropped with beans, sweet potato and fallow fields compared to the others. This may suggest that rodents might have a preference for certain food types such as sweet potatoes and maize which could sustain higher population abundances. This

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finding is in agreement with previous reports that showed higher small rodent abundances associated with maize and sweet potato (Mulungu et al. 2011, Hieronimo et al. 2014). On the other hand, the higher abundance in sugarcane and fallow fields may suggest that small rodent abundance is also highly influenced by habitats which form closed canopy and with limited human activity. Indeed, in Hawaii, the USA and Brazil significantly higher abundances of rodents were recovered in sugarcane compared to other crops causing considerable crop damage which researchers attributed to food preference and shelter from predation (Tobin et al. 1990, Gheler-Costa et al. 2012).

Vegetation characteristics as represented by NDVI also showed a relatively higher influence on small rodent abundance overall and within the individual districts. The influence of this particular variable may be attributed to food availability and cover. Earlier reports however ranked this variable very high with relative influence of over 80% on prediction of rodent abundance (Chidodo et al. 2020). The low relative influence reported in this study could be due to the short dry seasons characterized by the study location which sustain green vegetation almost all year round thus making the relative influence of this factor less important. Elsewhere NDVI has been studied and was shown to be a good indicator of primary productivity and cover, and it has long been employed to predict wildlife distribution and abundance, although mostly for larger mammals and in conservation areas (Pettorelli et al. 2011).

Soil physical composition including percentage silt, sand and clay was generally less important in predicting *M. natalensis* population abundance with only percentage composition of sand ranking relatively higher in importance. We found that abundance was higher at approximately 30-40% sand. Similarly, silt composition ranged between 40-90%. These proportional ranges qualify the soils to be classified as sandy loam following the United States Department of Agriculture (USDA) classification guide (Baillie 2001, Soil Survey Staff 1975, 1999). Indeed, sandy loam soils have been associated with supporting a variety of vegetative plants which offer food and cover to the rodents thus increasing survival and recruitment (Leirs et al. 1990, Mulungu et al. 2016). It has been demonstrated that sandy loamy soils have good aeration and are friable making them easier for the animals to burrow in (Massawe et al. 2008, Meliyo et al. 2015).

Our study also showed some discrepancy with rainfall ranking relatively low in importance in predicting rodent abundance. We attribute the results to the brevity of dry seasons relative to rainy seasons and thus insufficient seasonal variation in primary productivity significantly affect the rodent population. Leirs et al. (1997) reported that population abundance of small rodents tends to be affected where there are drastic clear seasonal variations between wet and dry seasons and where rodent populations are highly fluctuating.

Conclusion

This study has revealed that rodent abundance and richness in Uganda is governed by different landscape ecological factors. In terms of vegetation characteristics, NDVI appeared to be the key predictor for rodent abundance. In terms of soil characteristics the percentage of sand played a major role in predicting abundance. Crop type was an important predictor of both abundance and richness with sugarcane and fallow fields sustaining higher richness and abundance compared to the other crops. Our results have important implications for the management of small rodents, suggesting farmers should pay particular attention to sugarcane and fallow fields in their rodent management programs and increase control efforts in sites with heavy vegetation.

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