

# Small mammal species community structures vary by land use type in a Lassa fever endemic region of Sierra Leone.

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## Abstract

While the primary reservoir species of the zoonotic disease Lassa fever, the natal multimammate mouse (*Mastomys natalensis*), is considered abundant in anthropogenic habitats in West Africa, the detail of how rodent communities change over ecological gradients is not well understood. A more nuanced understanding how environmental change alters host zoonotic disease species' distributions and ecological assemblages is critical to quantify spatial hazard and to manage future emergence risk. Here, we investigate how rodent communities changed over a gradient of anthropogenic land use around 4 village study sites from 2020-2023, over 40,152 trap-nights, in Eastern Sierra Leone. We used a Bayesian multiple species occupancy model, accounting for imperfect detection, to show that *M. natalensis* were more likely to occur within villages of human habitation and agricultural land-use types than in forests and that there was a large variability in the probability of occurrence between different village study sites. *M. natalensis* co-occurred with other species including two invasive rodent species (*Rattus rattus* and *Mus musculus*). The presence of *M. musculus*, but not *R. rattus* reduced the probability of occurrence of *M. natalensis* in a different land use types. This finding may explain prior observations of lower-than-expected human cases of Lassa Fever from urban settings in endemic regions. We find a complex system of rodent species occurrence and co-location within human communities in Eastern Sierra Leone and further informs the quantification of the spatial hazard of *Lassa mammaronavirus* infection. Our findings highlight the spatially heterogeneous distribution of rodent species with implications for public health interventions to reduce the impact of Lassa fever.

## Introduction

Lassa fever, caused by *Lassa mammaronavirus* (LASV) is an endemic zoonotic infectious disease in West Africa. There are wide estimates of the annual number human of infections in the endemic region of between 100,000-4,383,600 (McCormick et al. 1987; Basinski et al. 2021). The majority of these infections remain undetected and it is estimated that, up-to 80% of these are pauci- or asymptomatic infections (McCormick et al. 1987). Few infections are expected to lead to clinically severe cases but outcomes in confirmed clinical cases remains poor. The case fatality rate, derived from reported deaths and reported cases is 16.5% (simons\_underreporting\_2022?). Anthropogenic land-use change and changing climate are hypothesised to increase the suitable area for both the primary reservoir of LASV (*Mastomys natalensis*) and environmental suitability for the virus itself (i.e. increased temperature and precipitation), together increasing opportunities for viral spillover into growing human populations (Redding et al. 2016, 2021; Klitting et al. 2021). Currently Lassa fever is currently considered endemic in eight West African countries (Nigeria, Guinea, Sierra Leone, Liberia, Mali, Benin, Ghana and Togo) (World Health Organisation 2022). The location, scale and frequency of Lassa fever outbreaks in human communities is highly spatially heterogeneous within these countries. For

example within Sierra Leone, Lassa Fever is typically reported from rural settings in the East of the country, the potential drivers of these spatial clustering patterns have not been systematically investigated.

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The persistence, or lack of persistence, of LASV infection in rodent communities may be one factor driving the observed spatial differences of outbreaks in human populations. In a well-mixed, isolated rodent population (i.e. rural settings), once introduced, LASV would be expected to rapidly infect susceptible populations. Infected rodents do not develop clinical symptoms, with antibody-mediated resistance to subsequent infections developing following an acute infection (ref?). This could lead to local elimination of the virus from these rodent populations as viral loads in infected individuals are reduced beyond the point of effective transmission [?]. Conversely in highly-connected, species depauperate rodent communities (i.e. urban settings) LASV persistence would be expected to be prolonged with viral transmission maintained through the rapid reproduction rate of rodents resulting in a large population of rodents susceptible to infection. In this way the suitability of both habitat type, climate and resource availability for both the primary reservoir and incidental reservoirs can drive the observed spatial clustering of Lassa Fever outbreaks within Sierra Leone.

*M. natalensis* is found in 13 of 14 continental West African nations (the species has not been reported from The Gambia) and in all other sub-Saharan African countries (IUCN 2016). It is considered a commensal rodent species and is abundant in and around areas of human-dominated landscapes where it is considered a pest species (Leirs, Verhagen, and Verheyen 1993). The introduction of non-native commensal rodent species (i.e. *Rattus rattus* and *Mus musculus*) has led to increased competition for resources and displacement of *M. natalensis* from some locations within its natural range (Cuyppers et al. 2017; Garba et al. 2014). Population dynamics within this reservoir species, correlated with resource availability and rainfall pulses (with increased abundance at the beginning of the dry season), are associated with outbreaks of Lassa fever in human populations (Redding et al. 2021). Few studies to date have used longitudinal, high intensity rodent trapping to characterise rodent species assemblages in Lassa fever endemic regions ((simons\_2022\_scoping?)). Understanding the true spatial distribution of *M. natalensis* and their population dynamics in the context of competing rodent species is vital to guide investigations of the epidemiology of Lassa fever (Basinski et al. 2021). Further, descriptions of rodent abundance and diversity along land use gradients are required to better understand the spatio-temporal hazard of Lassa Fever spillover under changing land use pressures (Klitting et al. 2021). The hazard of LASV spillover refers to the presence of competent host species in time and space, to better describe the risk of LASV outbreaks in human populations further information would be required that includes, pathogen prevalence within rodent hosts, and the probability of contact between susceptible human individuals and infectious rodents. Despite this limitation, understanding the hazard of LASV spillover can inform the implementation of contextually relevant public health responses, allocation of healthcare resources and the identification of suitable sites for future Lassa Fever vaccine studies.

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Here, we use data from a repeat, standardised, rodent trapping survey based in the Lassa Fever endemic region of Eastern Sierra Leone, conducted along a land-use gradient to understand the association between land-use on the occurrence of *M. natalensis* and more generally, the rodent species assemblage structure. We first report the occurrence of rodent species at our trapping sites and describe these species assemblages. Second, we model the association of land-use with the probability of species occupancy at trapping sites. Finally, we model the probability of co-occurrence between different species detected in our study to understand competition between small mammal species in our study region. Together these analyses further our understanding of rodent species assemblage structures in this heterogeneous landscape and the hazard of Lassa Fever outbreaks based on host species occurrence.

## Methods

### Data collection

We conducted rodent trapping surveys between October 2020-April 2023 within and around four village study sites (Baiaama; lat = 7.8375, long = -11.2683, Lalehun; lat = 8.1973, long = -11.0803, Lambayama; lat

= 7.8505, long = -11.1969, and Seilama; lat = 8.1224, long = -11.1936) in the Lassa fever endemic zone of the Eastern Province of Sierra Leone (Figure 1A.). **Figure 1A Sierra Leone in West Africa with the Eastern Province highlighted. Locations of village study sites within the Eastern Province as coloured points, consistent with colours used later.** Surveys were conducted in trapping grids along a land use gradient of anthropogenic disturbance comprising, forest, agriculture (including fallow and currently in use areas), and villages (within and outside of permanent structures) (See Supplementary Material 1 for images of trapping grid locations). Trapping grids were designated during the initial trapping survey session, one grid was deployed in forest land use, three to four grids were deployed in agricultural land with two grids deployed in village land use. For one village study site, Lambayama, there were no local forest areas, so this land use type was omitted (Figure 1B-E). **Figure 1B-E will show the locations of trapping grids within the villages.** Trapping survey sessions within each village occurred four times annually with two sessions in each of the rainy and dry seasons (May to November and December to April, respectively), giving a total of 10 trapping sessions over the study period.

Village study sites and trapping grids within the village study sites were selected to be representative of land use in the Eastern Province of Sierra Leone and based on accessibility to the sites during all seasons and acceptability of the study protocol to the village study site community. At each trapping grid 49 Sherman traps [size and reference] were placed in a 7 trap by 7 trap grid, traps were placed 10 metres apart in a regular grid conforming to the local landscape (mean area = 2208 m<sup>2</sup>) (Figure 1F). **Figure 1F will be a schematic of trapping grids.** For traps placed within permanent structures trap placement varied from this approach. Permanent structures were selected at random at each visit from a grid projected over the village area, with four traps placed within each structure. The location of each individual trap within trapping grids was geolocated for subsequent data processing. Traps were baited with a locally produced mixture of oats, palm oil and dried fish. Each morning the traps were checked and closed for the day prior to re-baiting during the evening. Each trapping survey session consisted of four consecutive trap nights (TN) at each trapping grid within the village study site. We collected a total of 40,152 trap-nights over 10 trapping visits between 2020-11-30 and 2023-04-28.

The location data of individual traps were harmonised to standardised trapping grid cells as a data cleaning step. First, the spatial extent of individual traps, with a 1 metre buffer, within a trapping grid across all trapping sessions was obtained. Second, a regular grid was constructed to overlay this area with a cell size of 49 m<sup>2</sup>, individual traps were allocated to this grid cell if they were contained within its borders. Finally, centroids of these grid cells were assigned to the trap to allow for aggregation over multiple trapping sessions. The `sf` package in the R statistical computing language was used for geospatial manipulation and analysis (Pebesma 2018; R Core Team 2021). The four consecutive trap nights obtained from each trap during a single survey are aggregated as a single replicate for the subsequent statistical analysis.

Trapped rodents were handled by trained fieldworkers, sedated with halothane and euthanised prior to obtaining morphological measurements and samples of blood and tissue (**reference to RVC and local ethics approval**) following published guidance (Fichet-Calvet 2014). The rodents sex was determined based on external and internal genitalia. Age estimation was performed through description of the rodents reproductive status (identification of perforate or imperforate vagina, scarring from prior embryo development, current pregnancy status or descent of testes and seminal vesicle development) and weighing of dried eye lenses [ref]. Carcasses were destroyed through incineration to eliminate risk of pathogen transmission.

Taxonomic identification was performed in the field based on external characteristics using an adapted taxonomic key (Supplementary Material 2.). This key included external morphological measurements and characteristics from Kingdon and Monadjem references, using the taxonomic references of ... Morphological identification is unable to distinguish multiple rodent species to sub-genera level. Therefore, molecular identification of individuals to species level was performed on whole blood or dried blood spots. Samples were stored at -20°C until processing, genomic DNA was extracted using QIAGEN DNAeasy kits as per the manufacturers instructions [ref]. DNA extracts were amplified using platinum *Taq* polymerase (Invitrogen) and cytochrome B primers [reference Elisabeths primers]. DNA amplification was assessed through gel electrophoresis with successful amplification products undergoing Sanger sequencing. Classification of obtained sequences was through BLAST compared to NCBI records for rodent cytochrome B [reference process].

## Analysis

### Description of rodent detection and species assemblage structure

Adequacy of trapping effort was assessed using species accumulation curves produced for each village study site and each land use type with a village study site (Supplementary Material 3.), suggesting sufficient effort to detect expected rodent species within each village site. We constructed detection/non-detection histories for each individual trap and rodent species, assigning “1” when the species was detected and “0” otherwise. We calculated species assemblages at multiple spatial scales. First, all species identified across all village sites and land use types. Second, all species identified within a village study site. Third, all species identified within a single land use type within a single village study site. We report species richness and Shannon diversity  $H$  at these different spatial scales (Equation 1.), where

$$H = - \sum (p_i) * \ln(p_i) \quad (1)$$

Here  $p_i$  is the proportion of the entire community made up of species  $i$ .

### Estimating the effect of land use on species occurrence and richness

To incorporate differential probabilities of detection that may be driven by environmental conditions during the trapping surveys and between species, we use a Bayesian multi-species occupancy framework to understand the association of small mammal species and land use types. Variable selection was informed from a pre-specified Directed Acyclic Graph (Supplementary Material 4.). Models were defined using the `spOccupancy` package in the R statistical computing language (Doser et al. 2022). This approach defines the true presence or absence ( $z$ ) of a species ( $i$ ), at site ( $j$ ) as arising from a Bernoulli process (Equation 2.). Where  $\psi_j$  is the probability of occurrence of a species at a site during a given replicate. This is modelled using a logit link where  $\beta_i$  are the regression coefficients, including an intercept that describes the effects of covariates  $\mathbf{x}_{i,j}$  with  $^\top$  representing the transposition of column vector  $\mathbf{x}_{i,j}$  (Equation 3.).

$$z_{i,j} \sim \text{Bernoulli}(\psi_{i,j}) \quad (2)$$

$$\text{logit}(\psi_{i,j}) = \mathbf{x}_{i,j}^\top \boldsymbol{\beta}_i \quad (3)$$

The regression coefficients in these multi-species occupancy models are described as random effects arising from a common community level distribution (Equation 4.). Where  $\boldsymbol{\mu}_\beta$  represents the community level mean effect for each occurrence covariate effect and  $\mathbf{T}_\beta$  is a diagonal matrix representing the variability of these among species in the community.

$$\boldsymbol{\beta}_i \sim \text{Normal}(\boldsymbol{\mu}_\beta, \mathbf{T}_\beta) \quad (4)$$

The detection component estimates the unobserved  $z_{i,j}$ . Here,  $y_{i,j,k}$  is the observed detection or non-detection of a species  $i$ , at site  $j$ , during replicate  $k$  (Equation 5.). This is approached as arising from a Bernoulli process conditional on the true latent occurrence process  $p_{i,j,k}$ . The probability of a species being detected at a site, during a replicate (given it is present at site  $j$ ), is a function of site and replicate specific covariates  $V$  and a set of species-specific regression coefficients  $\boldsymbol{\alpha}_i$  (Equation 6.).

$$y_{i,j,k} \sim \text{Bernoulli}(p_{i,j,k} z_{i,j}) \quad (5)$$

$$\text{logit}(p_{i,j,k}) = \mathbf{v}_{i,j,k}^\top \boldsymbol{\alpha}_i \quad (6)$$

Similarly to Equation 3., these coefficients are described as random effects arising from a common community level distribution, where  $\mu_\alpha$  represents the community level mean effect for each detection covariate effect and  $T_\alpha$  is a diagonal matrix representing the variability of these among species in the community (Equation 7.).

$$\alpha_i \sim \text{Normal}(\mu_\alpha, T_\alpha) \quad (7)$$

Minimally informative priors were specified for community and species level coefficients ( $\alpha$  and  $\beta$ , a normal prior of mean = 0, variance = 2.72) and for community level occurrence and detection variance parameters ( $T_\alpha$  and  $T_\beta$ , 0.1 for the scale and shape parameters of the inverse Gamma prior).

We included covariates in the model based on a pre-specified Directed Acyclic Graph and after assessing for co-linearity (defined as strong correlation >0.8) among variables (Supplementary Figure 2.). Continuous variables were standardised by scaling to values between 0-1. The fully specified model is defined in Equation 6 and 7.

$$\text{Probability of occurrence} \sim \text{Land use type} + \text{Village} + \text{scale}(\text{Distance to permanent structure}) + \text{scale}(\text{Distance to village centre}) \quad (8)$$

$$\text{Probability of detection} \sim \text{scale}(\text{Monthly precipitation}) + \text{Moon fraction} + \text{scale}(\text{Number of trap nights}) \quad (9)$$

Using this model, we estimate occupancy probability for each species in different land use types. Only estimates for species with detections from at least X trapping grid cells are included to avoid inference from limited data. We estimate species richness in each habitat type by obtaining the sum of species at a trapping site for each iteration of the Bayesian sampling process to compare rodent assemblage associations with land use classification.

### Co-occurrence of species (This approach may change)

To investigate the presence of competitive exclusion by rodent species in this setting we adopted a Binomial joint likelihood model fit using Integrated Nested Laplace Approximation (INLA) in the R statistical computing language (Rue, Martino, and Chopin 2009; Martins et al. 2013). Co-occurrence models were set up to estimate the probability of detection of two species  $\Gamma_a$  and  $\Gamma_b$  (Equation 10 and Equation 11). Here,  $\gamma$  is the species specific intercept for species  $a$  and  $b$  respectively.  $A.co.B$  and  $B.co.A$  represent the co-occurrence of species  $a$  with species  $b$  and species  $b$  with species  $a$  respectively.

$$\Gamma_a \sim \gamma_a + A.co.B \quad (10)$$

$$\Gamma_b \sim \gamma_b + B.co.A \quad (11)$$

Minimally informative priors were set for the intercept and species co-occurrence variables with a mean of 0 and precision of 1.

## Results

### Rodent occurrence and species assemblage structure

During the study period Y individuals were obtained from 40,152 trap-nights across the four village study sites (1.9% trap-success (TS)). The greatest number of individuals, highest species richness and Shannon diversity values were detected in agricultural land use type. The greatest TS was obtained from traps set within village land use (i.e. within and outside of permanent structures), although in these settings species

richness and Shannon diversity was lower (Table 1). The village study sites of Seilama and Lalehun had the highest overall TS, species richness and Shannon diversity although the land use types with the highest values of these metrics differed between the villages. Lambayama, the village study site located within the expanding boundaries of Kenema city, had the lowest species richness and Shannon diversity with the majority of rodents trapped within the village land use type.

Table 1. The number of individual small mammals (N), the number of trap nights (TN), trap-success (TS %), species richness and Shannon diversity by village and landuse type.

Village	Landuse	NTN (TS %)	Species richness	Shannon diversity
All villages				
	Village	1937972 (2.4%)	7	1.52
	Agriculture	29719168 (1.5%)	13	1.87
	Forest	393488 (1.1%)	8	1.63
Baiaama				
	Village	531552 (3.4%)	5	0.86
	Agriculture	323324 (1%)	8	1.67
	Forest	1980 (0.1%)	1	0.00
	Combined	865856 (1.5%)	9	1.46
Lalehun				
	Village	412100 (2%)	6	1.36
	Agriculture	815652 (1.4%)	9	1.69
	Forest	51176 (0.4%)	2	0.67
	Combined	1278928 (1.4%)	9	1.78
Lambayama				
	Village	651744 (3.7%)	4	0.49
	Agriculture	263920 (0.7%)	5	0.95
	Combined	915664 (1.6%)	6	1.05
Seilama				
	Village	342576 (1.3%)	6	1.52
	Agriculture	1586272 (2.5%)	10	1.81
	Forest	331332 (2.5%)	7	1.48
	Combined	22510180 (2.2%)	12	1.95

The most commonly detected rodent species across all village study sites and land use types was *M. natalensis* (N = 144, 19.2%), followed by *R. rattus* (N = 90, 12%), *M. musculus* (N = 86, 11.5%) and *Lophuromys rostratus* (N = 74, 9.9%) (Supplementary Material 5.). *M. natalensis* and *R. rattus* were detected in all village study sites *M. natalensis* was not detected in forest land use types (Figure 2.). Conversely, *Hybomys planifrons* and *Gerbilliscus kempii* were only detected in a single village study site, with *H. planifrons* detected in forest land use and *G. kempii* in agricultural land use types. The invasive rodent species *M. musculus* was only detected in Lambayama and Seilama village study sites within village land use types. The detection

rate (the number of individuals detected per 1000 TN) varied by species, land use type and village study site. The greatest rate of detection was for *M. musculus* in the Lambayama village study site, with the other commensal species *M. natalensis* and *R. rattus* high across multiple village study sites within village land use types. *Praomys spp.* and *Crocidura spp.* had the highest detection rates in forest and agricultural land use types.

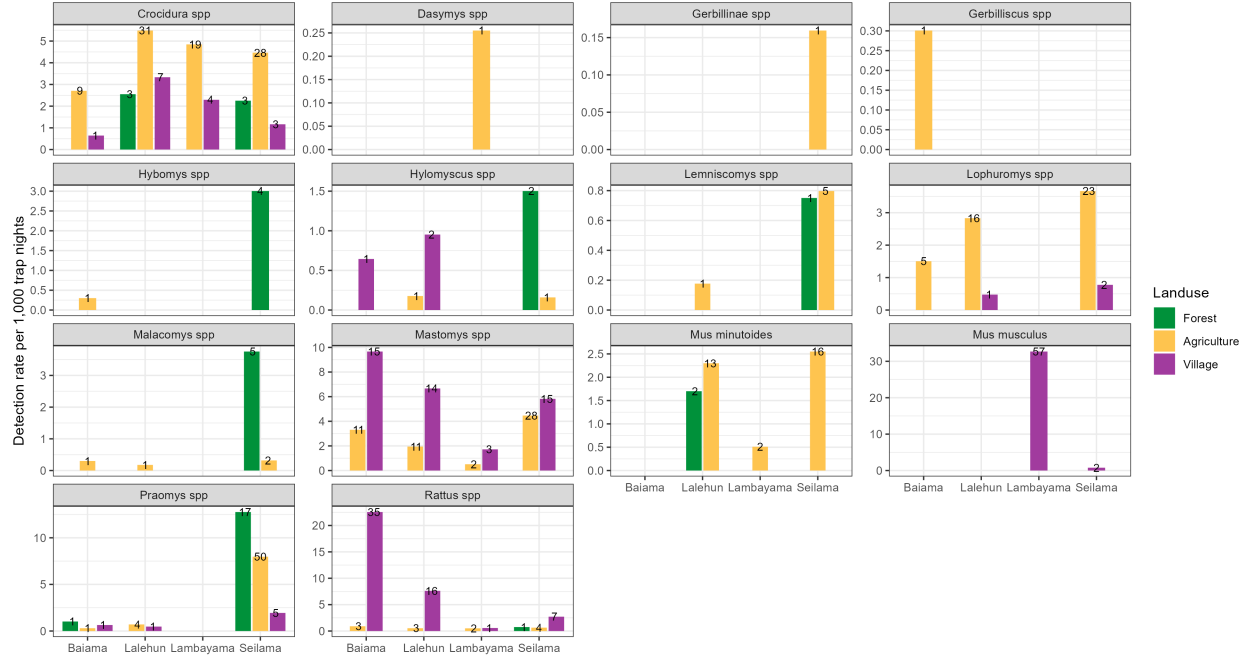


Figure 2. Detection rate of rodent species in land use type. The detection rate per 1000 TN and the number of detections of each rodent species in the three land use types across all four village study sites are shown. The scale for detection rate per 1000 TN on the y-axis varies by species. The number on the column is the number of individuals trapped within this setting. The greater rate of detection of *M. musculus* within village land use types are clearly shown with the other commensal rodent species being detected more frequently in non-village land use types and across more village study sites. Rodent species that were not detected in village land use types were generally less frequently detected throughout the study (i.e. *Lemniscomys spp.*, *Malacomys spp.* and *M. minutoides*)

There was little observed variation in species richness by season. The prevalence of a species (measured as the number of positive detections for a constant trapping effort), was reduced for most species during the rainy season, except for *M. natalensis* which was more often detected in village land use types during the rainy season compared to the dry season (Supplementary Material 6.).

## Estimating the effect of land use on species occurrence and richness

Posterior samples were drawn from the most parsimonious Bayesian occupancy model incorporating spatial autocorrelation (Supplementary Material 7.). Occurrence terms include land use type, village study site as a fixed effect, and terms for distance to the nearest permanent structure and elevation. Detection terms include precipitation, trapping effort (TN) and the moon fraction. We found three patterns of probability of occurrence ( $\psi$ ) within a trapping grid cell for the seven included species with more than 10 detection across the different land use types (Figure 3.). First, *Praomys spp.* had higher probability of occurrence in forest land use with lower probabilities in agricultural and village land use types. Second, *Crocidura sp.*, *Lophuromys sp.* and *Mus minutoides* had highest probabilities of occurrence in agricultural land use with lower probabilities of occurrence in forest and village land use. Third, *M. natalensis*, *R. rattus* and *M. musculus* had highest probabilities of occurrence in village land use with lower occurrence probabilities in

agricultural and village land use types. No species showed high probability of occurrence across all land use types, consistent with species being adapted to distinct ecological niches.

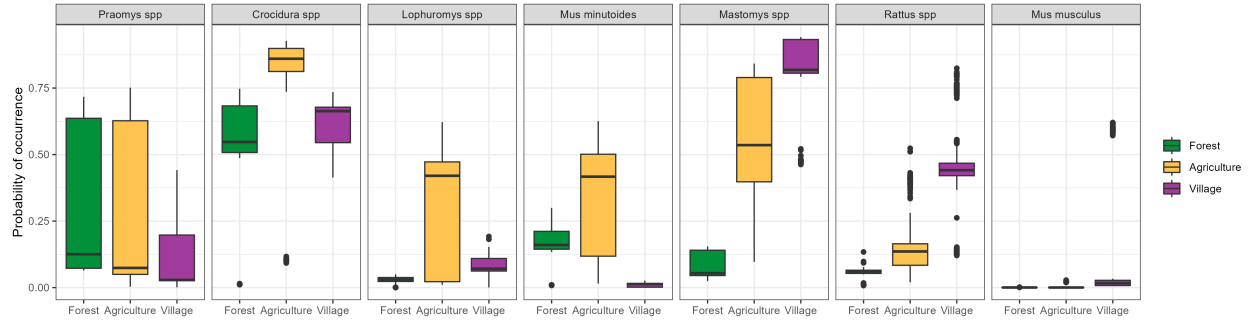


Figure 3. Probability of species occurrence across a land use gradient. The probability of occurrence ( $\psi$ ), within different land use types, for the seven small mammal species with more than 10 detections is shown. The solid black horizontal line within the boxplot is the median values of the samples from the posterior distribution of  $\psi$ . The hinges represent the 25th and 75th percentiles. Black points represent outliers to the box plots.

The probability of occurrence within a trapping grid cell of some species within the same land use types differed by village study site as suggested by the outliers in Figure 3. For example, the probability of occurrence of *Praomys spp.* at trapping grid cells within forest (median = 0.64, Inter-Quartile Range (IQR) = 0.001) and agricultural (median = 0.64, IQR = 0.04) land use types is greater at Seilama village study site than at the same land use types in other village study sites (median < 0.13). For the commensal rodent species *M. natalensis* and *R. rattus* probability of occurrence followed a consistent pattern of higher probability of occurrence within village land use than compared to agricultural land use within village study sites, although probabilities were lower for the Lambayama village study site. For *M. musculus* the probability of occurrence was generally low in all land use types except village land use at the Lambayama village study site. The occurrence probabilities for these three commensal species (*M. natalensis*, *R. rattus* and *M. musculus*) suggest that competition may be reducing the occurrence of *M. natalensis* and *R. rattus* in the presence of *M. musculus* which in its absence have high occurrence probabilities in village land use types.

I am not sure the best representation for this section. Does it work better as land use type split by village for each species (A) or by village study site split by land use type for each species (B)? An alternative representation would be splitting by urbanisation based on human population density at the sites which splits it into Lambayama as the peri-urban and all others as rural (C). All convey the same data it's just trying to decide which is a clearer representation of the message.

### Co-occurrence of species (Needs more work)

We found that species co-occurrence differed between species pairs. The probability of occurrence of *M. natalensis* in the absence of *M. musculus* was 0.28, the presence of *M. musculus* at a nearby trapping grid reduced this to 0.16. This antagonism was greater than that observed for another invasive rodent species *R. rattus* where probability of occurrence of *M. natalensis* in the absence of *R. rattus* was 0.24, the presence of *R. rattus* reduced this to 0.18. These findings further suggest a strong displacement effect of *M. musculus* which is not seen with *R. rattus* at our study sites.

### Discussion (Bullet points for now)

Here, we have presented the results from a systematic small-mammal trapping study in Eastern Sierra Leone performed to characterise the rodent species assemblages in a Lassa fever endemic region. We found that



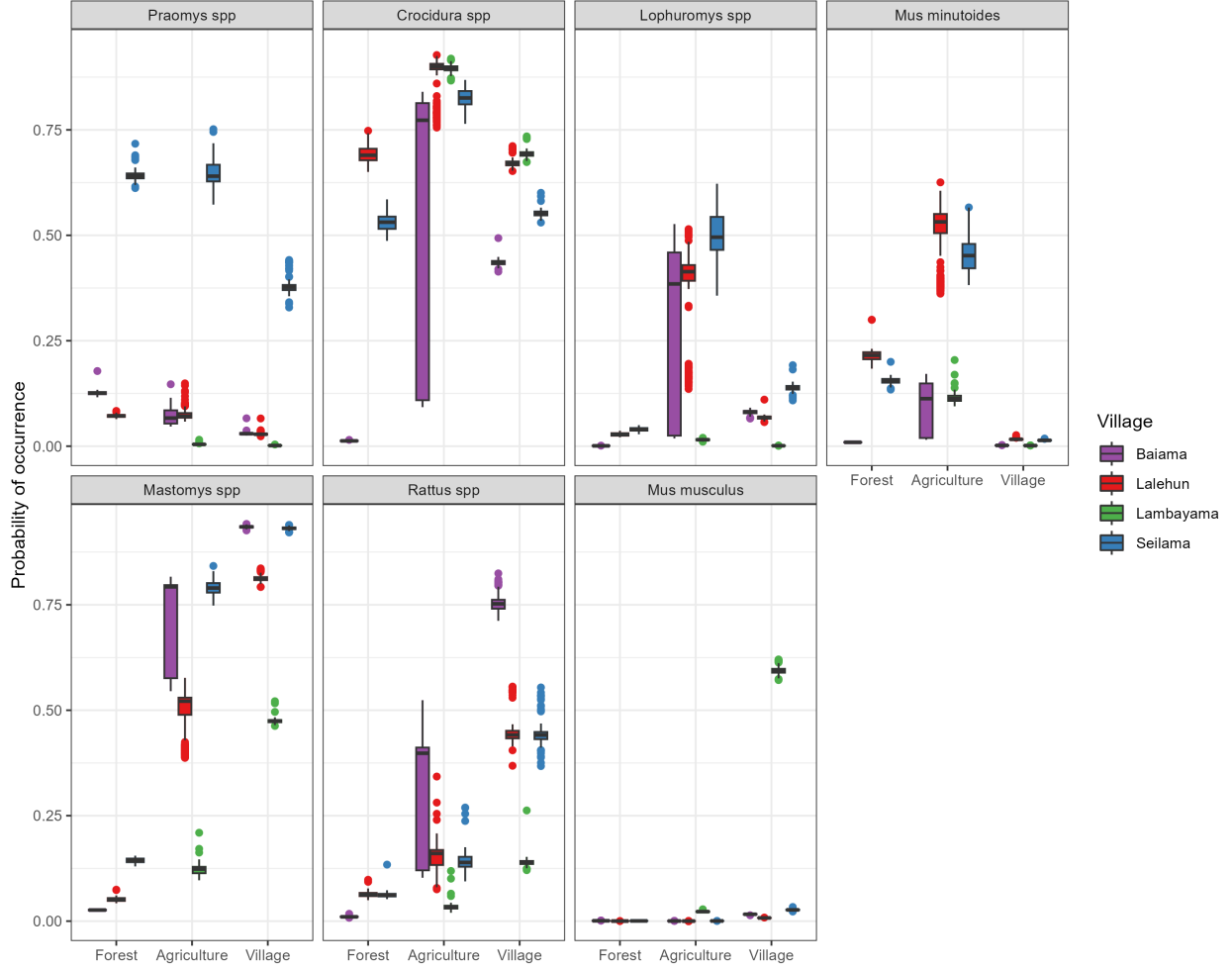


Figure 4. Probability of species occurrence across a land use gradient by village study site. The probability of occurrence ( $\psi$ ), within different land use types, for the seven small mammal species with more than 10 detections is shown. The solid black horizontal line within the boxplot is the median values of the samples from the posterior distribution of  $\psi$ . The hinges represent the 25th and 75th percentiles. Black points represent outliers to the box plots.

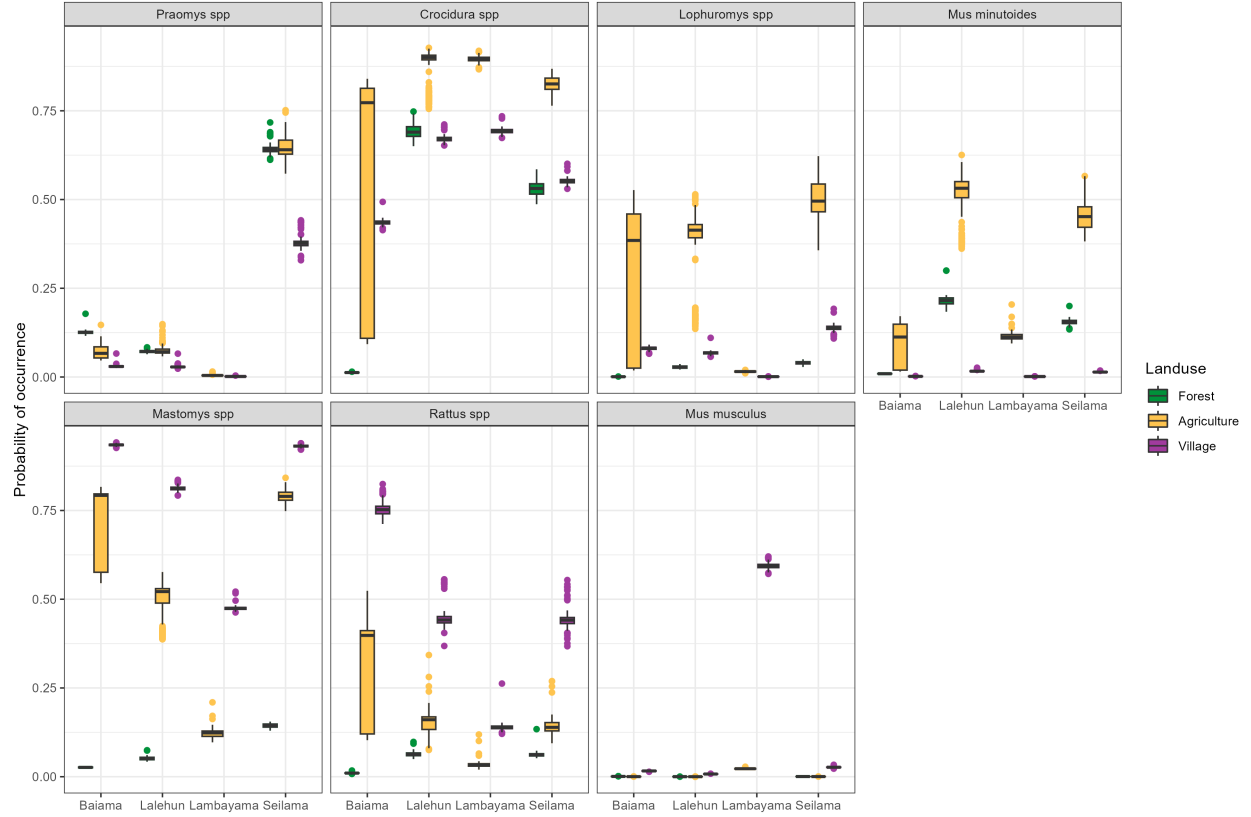


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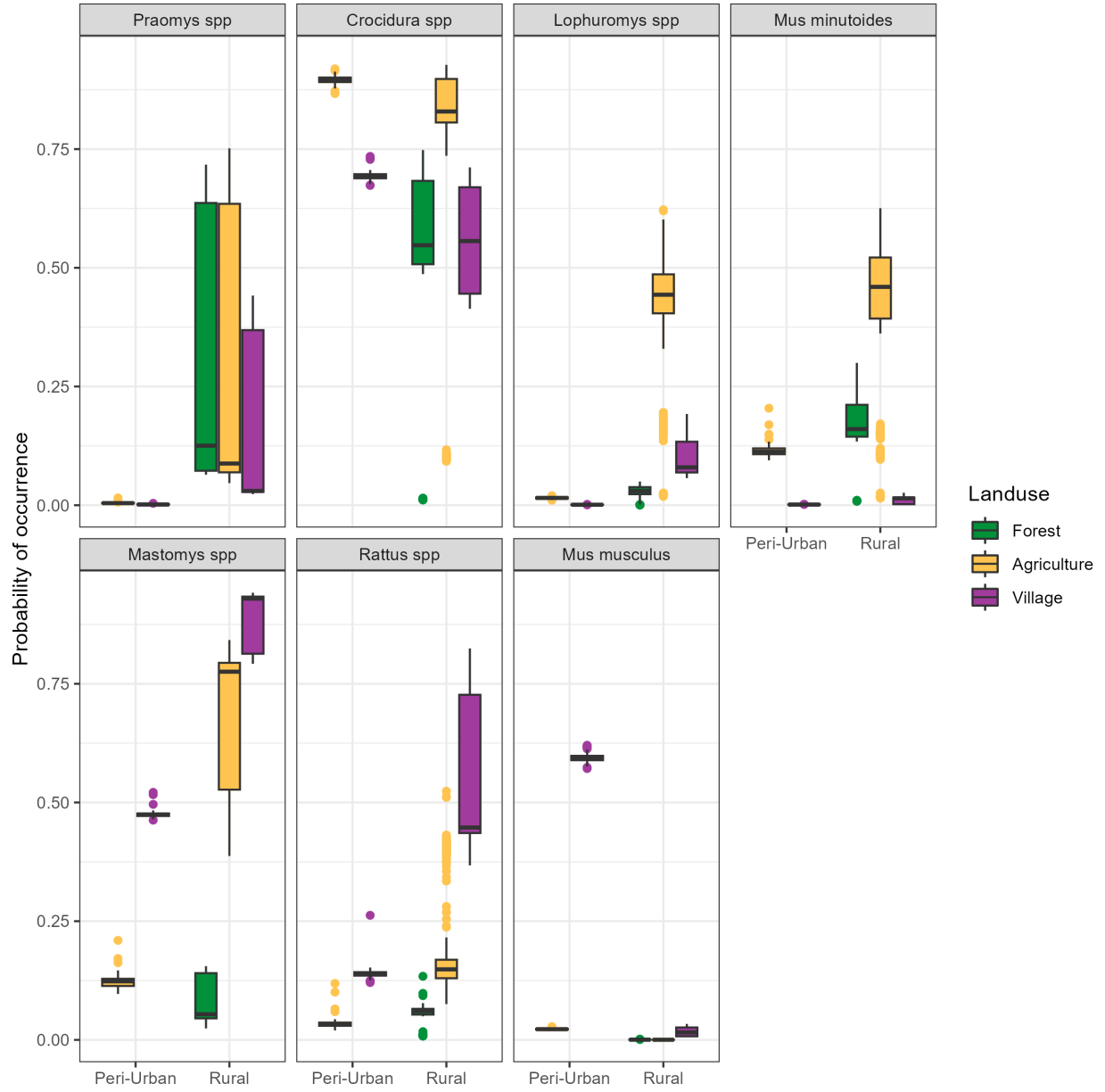


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species richness and diversity is greater than that reported from other regions of the Lassa fever endemic zone and that there is a strong association of land-use on the species composition of these rodent assemblages.

Rodent species richness was found to be greatest in agricultural settings where small-mammals with greatest occurrence in human dominated land-use types and those in forested settings were found to occur. These settings may provide opportunity for *Lassa mammaronavirus* transmission between rodent species and providing a method for introduction of the virus into populations with limited dispersal ranges. Within human dominated settings

The segregation of rodent species into distinct ecological niches of human dominated (village and agriculture) or non-human dominated (forest) settings may have implications for the movement of individuals of these species across the landscape in the fractured habitats of Eastern Sierra Leone. This may have important implications for the transmission of pathogens, such as *Lassa mammaronavirus*, if competent reservoirs exist in disconnected populations.

Across most of our village study sites we identified high occurrence of the principle rodent reservoir of *Lassa mammaronavirus* with this species concentrated in areas of significant anthropogenic disturbance (i.e. Villages, within and outside of buildings and in agricultural land). However, in Lambayama, our most urban site this species was found to have low occurrence with probable displacement by the invasive rodent *M. musculus*. These findings suggest that the hazard of human exposure to *Lassa mammaronavirus* is concentrated in more rural village settings and in those villages at low risk of *M. musculus* invasion and establishment.

## Conclusion

We present data on rodent species assemblages within a Lassa fever endemic region and identify high occurrence of rodent species suitable as reservoirs for *Lassa mammaronavirus* which vary importantly by land-use type and village study site. We are able to recreate potential contact networks between individual rodents within these settings which may explain the spatial and temporal heterogeneity of Lassa fever outbreaks in endemic regions. Further research is required to link these rodent population structures with viral transmission in these landscapes.

## Supplementary figures.

## References

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