Land use gradients drive spatial variation in Lassa fever host communities in the Eastern Province of Sierra Leone.

Author details.

David Simons [1,2,3], Rory Gibb [2,4], Umaru Bangura [5,6], Dianah Sondufu [6], Joyce Lamin [6], James Koninga [7], Momoh Jimmy [7], Mike Dawson [6], Joseph Lahai [6], Rashid Ansumana [6], Elisabeth Fichet-Calvet [5], Deborah Watson-Jones [3,8], Richard Kock [1], Kate E. Jones [2,4].

[1] Centre for Emerging, Endemic and Exotic Diseases, The Royal Veterinary College, London, United Kingdom

[2] Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, London, United Kingdom

[3] Clinical Research Department, London School of Hygiene and Tropical Medicine, London, United Kingdom

[4] People & Nature Lab, UCL East, Department of Genetics, Evolution and Environment, University College London, London, United Kingdom

[5] Bernard-Nocht Institute for Tropical Medicine, WHO Collaborating Centre for Arbovirus and Hemorrhagic Fever Reference and Research, 20359 Hamburg, Germany

[6] Njala University, Bo, Sierra Leone

[7] Kenema Government Hospital, Kenema, Sierra Leone

[8] Mwanza Intervention Trials Unit, National Institute for Medical Research, Mwanza, Tanzania

Corresponding author email: dsimons19@rvc.ac.uk

Acknowledgments

DS, RA, EF-C and RK acknowledge support from the Pan-African Network on Emerging and Re-Emerging Infections (PANDORA-ID-NET; https://www.pandora-id.net/) funded by the European and Developing Countries Clinical Trials Partnership (EDCTP) within the EU Horizon 2020 Framework Programme. DS was supported by a PhD studentship from the UK Biotechnology and Biological Sciences Research Council (BB/M009513/1). KEJ is supported by funding from the Trinity Challenge (The Sentinel Forecasting Project).

The authors would like to thank Jeff Doser, the developer of the `spOccupancy` package for assistance with optimising the model construction and fitting process.

Conflict of interest

All authors report no financial conflicts of interest.

Authors' contributions

DS, RG, EF-C, DW-J, RK and KEJ conceived the ideas and designed the methodology. DS, UB, DiS, JL, JK, MJ, MD, JoL and RA collected the data. DS and RG analysed the data. DS, RG and KEJ interpreted the analysis. DS, UB, EF-C, DW-J, RK and KEJ provided supervision and resources to conduct the study. DS led the writing of the manuscript. RG, DW-J, RK and KEJ contributed critically to the drafts. All authors gave final approval for publication.

Statement on inclusion

This study brings together authors from several countries, including scientists based in the country where the study was carried out. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent was considered. Literature published by scientists from the study country and wider region was cited. Study protocols were discussed with local scientists for appropriateness of design. Consultations were held with community leaders of the study villages and the wider region before finalising the study design and enrolment of sites into the study.

Data availability

Data on detected rodent individuals are available on PHAROS (https://pharos.viralemergence.org/projects/?prj=prjyg91YQvrdk).

All R scripts and data to reproduce the analysis are available on GitHub (https://github.com/DidDrog11/land-use-lassa-hosts).

Word count: 7,755

Abstract

1. The natal multimammate mouse (*Mastomys natalensis*) is the primary reservoir host of *Lassa mammarenavirus* (LASV), a zoonotic pathogen causing Lassa fever that is endemic to West Africa. The occurrence and abundance of this species is regulated by the human environment and biotic interactions with other small-mammal species, but these ecological drivers remain poorly understood in the regions where Lassa fever outbreaks are observed.
2. We developed a Bayesian multi-species occupancy model incorporating incomplete detection to assess habitat use from data obtained as part of a multi-year small-mammal trapping study (43,226 trap nights across four village sites in Sierra Leone, 2020-2023). We investigated the effects of land use gradients and small-mammal community dynamics on the spatial distribution of *M. natalensis*.
3. *Mastomys natalensis* occupancy increased along a gradient from forest to agriculture to village habitats but was reduced in peri-urban settings compared to rural settings. Invasive rodent species influenced this pattern, with *Mus musculus* presence associated with reduced *M. natalensis* occupancy in peri-urban settings. We did not observe a similar effect when considering the co-occurrence of invasive *Rattus rattus* with *M. natalensis* in rural settings.
4. These findings suggest that land use and species interactions drive spatial heterogeneity in *M. natalensis* populations, potentially explaining reduced Lassa fever incidence in urban areas. The results highlight the importance of considering

community dynamics when predicting the risk of outbreaks of endemic zoonoses and the need to widen the context of studies of LASV transmission beyond the primary reservoir host species.

5. To better assess public health risk and improve allocation of limited resources, we recommend more precise characterisation of small-mammal communities in LASV endemic regions, particularly in areas undergoing rapid land use change which may alter community level small-mammal biodiversity.

Introduction

Global biodiversity is in decline, with biodiversity loss directly influencing zoonotic disease risk (Sala et al. 2000; Mantyka-Pringle et al. 2015; IPBES 2020). Land use change, particularly the conversion of natural habitats into agricultural or urban landscapes, is a key driver of biodiversity loss, reducing mammalian species diversity across several dimensions (Newbold et al. 2015). These include taxonomic diversity (the number and relative abundance of taxa), functional biodiversity (an increase in the abundance of generalist, synanthropic animals) and interaction diversity (the biotic interactions among species) (Naeem, Duffy, and Zavaleta 2012; Glidden et al. 2021). These declines in biodiversity, particularly in rodent-associated disease systems, may exacerbate zoonotic disease risks by promoting the proliferation of generalist, synanthropic rodents that thrive in human-modified landscapes, where they host zoonotic pathogens (Young et al. 2014; Gibb et al. 2020; Ecke et al. 2022). This shift may therefore not only increase the prevalence of zoonotic pathogens but also human exposure in complex socio-ecological systems (Gibb et al. 2025).

The role of host community diversity in mediating zoonotic outbreaks is nuanced, with changes in species composition and pathogen prevalence often interacting with anthropogenic stressors to create context-specific outcomes (Gibb et al. 2020; Keesing and Ostfeld 2021; Carlson et al. 2025). A deeper mechanistic understanding of these processes, including community structure, biotic interactions, and responses to anthropogenic land use change, is critical for leveraging biodiversity knowledge to predict and mitigate zoonotic risks (Salkeld, Padgett, and Jones 2013; Glidden et al. 2021; Carlson et al. 2025). These approaches have only been taken for a few rodent associated zoonoses (Keesing and Ostfeld 2024).

Rodents are an important mammalian host taxa for zoonotic diseases (Han et al. 2015; Mendoza et al. 2019). Rodent-associated zoonoses, such as Lyme disease caused by *Borrelia burgdorferi sensu lato*, have been shown to involve a complex interplay of community structure, biotic interactions, and the effect of land use change (Ostfeld and Holt 2004). For instance, land use change can increase reservoir abundance and subsequently zoonotic risk, though responses vary across systems and settings, highlighting the idosyncratic or system specific nature of these dynamics (Young et al. 2017; Mendoza et al. 2019; Pei et al. 2024).

Lassa fever, caused by *Lassa mammarenavirus* (LASV), is an important rodent-associated zoonosis endemic to West Africa, reported from Nigeria, Guinea, Sierra Leone, Liberia, Mali, Benin, Ghana and Togo and causes an estimated 900,000 annual infections with substantial morbidity and mortality (World Health Organisation 2022; Basinski et al. 2021). Risk of infection in human populations is spatially heterogeneous with patchy distributions of reported cases across the endemic region (Gibb et al. 2017; Agbonlahor et al. 2021; Grant et al. 2023). While epidemiological factors such as acquired immunity and asymptomatic infections may contribute, reservoir host ecology and distribution are likely critical drivers of this variation (McCormick et al. 1987).

Mastomys natalensis, considered the main reservoir host, is a synanthropic rodent species found throughout sub-Saharan Africa (IUCN 2016). It is abundant in and around areas of human-dominated landscapes where it is considered a pest species (Leirs, Verhagen, and Verheyen 1993). Population dynamics in *M. natalensis* are influenced by resource availability and seasonal rainfall pulses, which drive fluctuations in abundance that coincide with increased human Lassa fever outbreaks (Leirs et al. 1996; Leirs et al. 1997; Redding et al. 2021). However, most intensive ecological studies of *M. natalensis* have been conducted outside the Lassa fever endemic region, in regions with differing agro-ecologies, potentially limiting their applicability to West Africa (Leirs et al. 1996). The effects of land use change on rodent communities in the endemic region have only been explored across a limited geographic area, with most studies focusing solely on the role of the rodent reservoir (Fichet-Calvet et al. 2005, 2014; Fichet-Calvet et al. 2009; Olayemi et al. 2018; Arruda et al. 2021). The limited number of studies that do consider the wider rodent community typically focus on abundance (measured through summary proxies such as trap-success) rather than explicitly investigating community dynamics (Fichet-Calvet et al. 2009; Eskew et al. 2024).

There is a pressing need for systematic small-mammal community studies in West Africa to ensure generalisability of these findings to Lassa fever, and to disentangle the respective roles of abiotic factors, such as land use type, and biotic interactions within small-mammal communities in shaping *M. natalensis* distributions and pathogen exposure risks. *Mastomys natalensis* occurs within species rich settings in West Africa, biotic interactions between this species and other native and invasive rodents within communities and how these may regulate *M. natalensis* occurrence are not well described (Fichet-Calvet et al. 2009; Garba et al. 2014; Cuypers et al. 2017; Hima et al. 2019). Past studies have indicated that competitive interactions with *R. rattus* and *M. musculus* can alter native rodent communities, and might therefore reshape *M. natalensis* local distributions with subsequent effects on LASV transmission and Lassa fever hazard (Dalecky et al. 2015; Lippens et al. 2017; Eskew et al. 2024). Sierra Leone is associated with frequent outbreaks of Lassa fever in human populations, with evidence of outbreaks beyond the traditionally accepted endemic region with limited evidence for how community dynamics (i.e., occurrence of invasive rodent species) might influence these (Monath et al. 1974; Keenlyside et al. 1983; McCormick et al. 1987; Bonner et al. 2007; Bonwitt et al. 2017; Bangura et al. 2021; Grant et al. 2023; Eskew et al. 2024).

Given these gaps in understanding, we sought to explore how small-mammal communities are structured across land use gradients in Eastern Sierra Leone and how these dynamics influence the distribution of *M. natalensis*. To achieve this we conducted repeated, systematic, rodent trapping along a land use gradient in Eastern Sierra Leone to investigate how land use influences small-mammal communities and the distribution of *M. natalensis*. We hypothesised that: (1) small-mammal community diversity varies with land use, with lower diversity in more anthropogenic habitats; (2) *M. natalensis* occupancy is positively associated with anthropogenic land use but negatively influenced by competition with sympatric species; and (3) species interactions within small-mammal communities regulate the local distribution of *M. natalensis*, thereby shaping LASV outbreak risk. Sierra Leone, a hotspot for Lassa fever, provides a unique opportunity to explore these dynamics in a region where rodent ecology studies have largely focused on *M. natalensis*, often neglecting the broader small-mammal community. We expect these analyses to further understanding of small-mammal community structures that may explain observed patterns of LASV outbreaks within this context and the wider endemic region.

Methods

Small-mammal sampling

We conducted small-mammal trapping surveys from October 2020 to April 2023 at four village study sites (Baiama, Lalehun, Lambayama, and Seilama) located in the Lassa fever endemic zone of Sierra Leone's Eastern Province (Figure 1A). Site selection was informed by discussions with the Kenema Government Hospital Lassa Fever team and guided by remote imaging data to ensure representation of prior disease outbreak areas. Trapping grids were established along a gradient of anthropogenic disturbance, encompassing forest, agricultural land (both fallow and active), and village areas (inside and outside permanent structures). Each village study site was assigned one forest grid, three to four agricultural grids, and two village grids, except for Lambayama, which lacked forested land (Supplementary Figure 1 A-D). Trapping survey sessions within each village occurred four times annually with two trapping surveys in each of the rainy and dry seasons (May to November and December to April, respectively), producing a total of 10 trapping sessions over the study period (Figure 1B).

We selected village study sites and trapping grids within the village study sites 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 communities (Supplementary Information 1). Trapping grids consisted of 49 Sherman traps (7.62 × 8.89 × 22.86 cm; H.B. Sherman Traps, Tallahassee, USA), arranged in a 7 × 7 layout with 7-metre spacing between traps, adjusted to the local terrain (median grid area = 3,882 m^2). For grids within permanent structures, the grid arrangement was modified: individual buildings were semi-randomly selected using a projected village grid, and four traps were deployed per 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 standardised individual trap locations to 49 m^2 trapping grid cells for analysis. First, a convex hull encompassing all trapping sessions for a grid was generated. A regular 49 m^2 grid was overlaid on this polygon, and traps were assigned to cells based on their spatial coordinates. This process resulted in 2,068 unique grid cells across all sites (Supplementary Figure 2). Geospatial processing was performed using the `sf` package R (version 4.1.2) (Pebesma 2018; R Core Team 2021). The four consecutive trap-nights obtained from each trap during a single survey are pooled as a single replicate (i.e., trapping session) for the subsequent statistical analysis.

All small mammals were handled by trained researchers wearing appropriate personal protective equipment. Animals were sedated using halothane and euthanized according to established protocols (Fichet-Calvet 2014). Morphological measurements and samples of blood and tissue were collected. The study was approved by the Clinical Research Ethical Review Board and Animal Welfare Ethical Review Board of the Royal Veterinary College, UK (URN: 2019 1949-3), and the ethical review board of Njala University, Sierra Leone, and adhered to national and institutional ethical guidelines. Sex was determined based on external and internal genitalia. Age classification was informed by reproductive status (e.g., perforate vs. imperforate vagina, scarring from prior pregnancies, current pregnancy status, descended testes, and seminal vesicle development) and lens weight from dried eye samples. Photographs of the dorsal and ventral aspects of each rodent were taken for morphological documentation. All carcasses were incinerated to mitigate pathogen transmission risks.

Species classification

Species identification was performed in the field based on external morphological characteristics, including body length, tail length, ear length, and pelage colouration, following the taxonomic keys of Kingdon and Happold (Kingdon and Happold 2013) and Monadjem *et al.* (Monadjem et al. 2015) (Supplementary Information 2). Field identification was supplemented by molecular methods to confirm species identity for individuals identified as *Mastomys sp.*, *Mus sp.*, *Rattus sp.* and *Crocidura sp.* alongside a random subset of remaining individuals (50% of remaining samples).

Samples were stored at -20°C until processing and genomic DNA was extracted using QIAGEN DNAeasy kits as per the manufacturers instructions (QIAGEN 2023) (Supplementary Information 1). DNA extracts were amplified via polymerase chain reaction (PCR) using *cytochrome B* primers, and amplification success was confirmed via gel electrophoresis (Bangura et al. 2021). Full details of the PCR and sequencing protocols, including thermocycler settings, are provided in Supplementary Information 1. Successful PCR products were purified and submitted for Sanger sequencing (performed by Eurofins Genomics). Attribution of sequences to rodent species was performed using the BLAST programme, comparing obtained sequences to *cytochrome B* records in the NCBI database (accessed 2023-06-30) (Altschul et al. 1990).

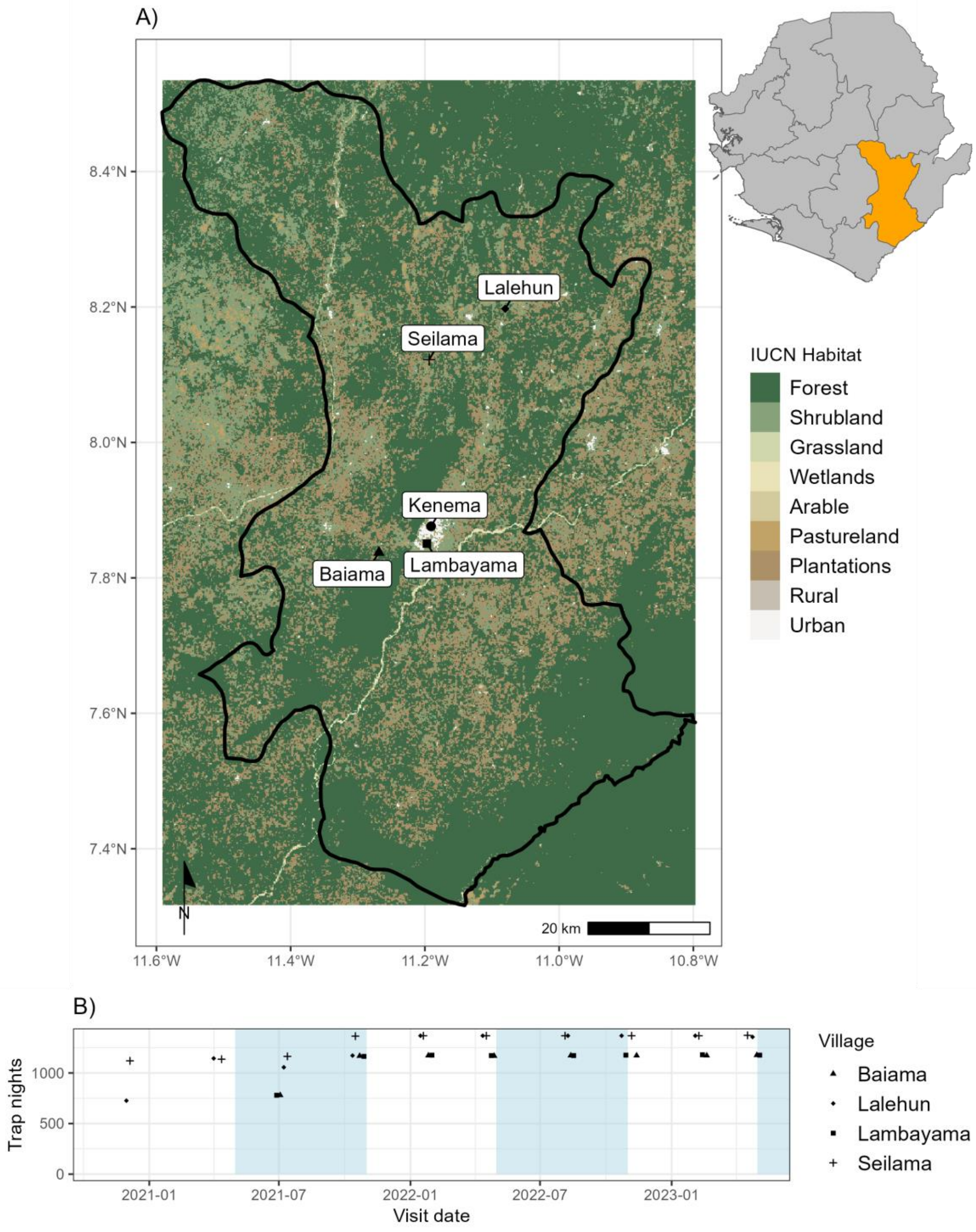

***Figure 1**: Village site locations and dates of rodent trapping in Sierra Leone. A) Location of village study sites (coloured labels), in the Eastern Province of Sierra Leone, Kenema, the largest city of the province is shown with a white label. The inset map shows the location of Sierra Leone in West Africa. B) Number of trap nights obtained from each study village, blue shaded regions represent the rainy season in Sierra Leone. The background raster image of Eastern Province, Sierra Leone was adapted from data presented in Jung et al. 2020. Shapefiles of Sierra Leone and administrative districts were obtained from GADM, 2022.*

Description of small-mammal detection and species community structure

Adequacy of sampling effort was assessed using species accumulation curves produced for each village study site and each land use type within a village study site, generated with the `specaccum` function from the vegan package (Oksanen et al. 2022). The rarefaction method was applied to evaluate whether sampling was sufficient to detect the expected rodent species within these categories. Curves were visually inspected, and most demonstrated a plateau, suggesting adequate sampling effort (Supplementary Figure 3).

Detection/non-detection histories for each grid cell and small-mammal species were constructed, assigning “1” when a species was detected and “0” otherwise. Species communities were described at multiple spatial scales: (i) all species identified across all village sites and land use types, (ii) all species identified within a village study site, and (iii) all species identified within a single land use type within a single village study site. Species richness and Shannon diversity were calculated at each of these spatial scales (Shannon 1948).

Estimating the effect of land use on species occurrence and richness

To adjust for differential probabilities of detection that may be driven by environmental conditions and trapping effort during the trapping study and between species, we use a Bayesian spatial latent factor multi-species occupancy model that incorporates residual species correlations, imperfect detection and spatial autocorrelation. Variable selection was informed by a pre-specified conceptual model (Supplementary Figure 4). Models were defined using the `sfMsPGOcc` function in 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 grid cell ($_j$) as arising from a Bernoulli process (Equation 1). Where ψ_j is the probability of occurrence of a species at a grid cell. This is modelled using a logit link where β_i are the species-specific regression coefficients of the site-specific covariates ($\mathbf{x}_j^\top$) and a latent process $\mathrm{w}_{i,j}^*$. This latent process incorporates residual species correlations through a small number of latent spatial factors and latent variables representing unmeasured grid cell covariates (Equation 2). Latent spatial factors account for spatial autocorrelation using a Nearest Neighbour Gaussian Process.

$$z_{i,j} \sim \mathrm{Bernoulli}\left(\psi_{i,j}\right) \qquad \text{(Equation 1)}$$

$$\mathrm{logit}\left(\psi_{i,j}\right) = \mathbf{x}_j^\top \boldsymbol{\beta}_\mathbf{i} + \mathrm{w}_{i,j}^* \qquad \text{(Equation 2)}$$

The species-specific regression coefficients (β_i) are specified as random effects arising from a common community level distribution (Equation 3). 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 the species in the community.

$$\boldsymbol{\beta}_i \sim \mathrm{Normal}\left(\boldsymbol{\mu}_\beta, \mathbf{T}_\beta\right) \qquad \text{(Equation 3)}$$

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 4). 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 grid cell, during a replicate (given it is present at grid cell j), is a function of grid cell and replicate specific covariates $\mathbf{v}$ and a set of species-specific regression coefficients $\boldsymbol{\alpha}_i$ (Equation 6).

$$y_{i,j,k} \sim \text{Bernoulli}(p_{i,j,k} z_{i,j}) \qquad \text{(Equation 4)}$$

$$\text{logit}(p_{i,j,k}) = \mathbf{v}_{i,j,k}^{\mathsf{T}} \boldsymbol{\alpha}_i \qquad \text{(Equation 5)}$$

Similarly to Equation 3, these coefficients are specified as random effects arising from a common community level distribution, where $\boldsymbol{\mu}_\alpha$ represents the community level mean effect for each detection covariate effect and $\mathbf{T}_\alpha$ is a diagonal matrix representing the variability of these among species in the community (Equation 6).

$$\boldsymbol{\alpha}_i \sim \text{Normal}(\boldsymbol{\mu}_\alpha, \mathbf{T}_\alpha) \qquad \text{(Equation 6)}$$

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

We included covariates in the model based on a pre-specified conceptual model and after assessing for co-linearity (defined as strong correlation >0.8) among variables. Continuous variables were standardised by scaling values between 0-1. The fully specified model is defined in Equation 7 and 8 and using a single latent spatial factor.

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

(Equation 7)

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

(Equation 8)

Model checks, including mixing patterns of the MCMC sampler and posterior predictive checks, were performed as an assessment of goodness of fit. Bayesian p-values were calculated for both community-level and species-level fits, with values between 0.1 and 0.9 suggesting an adequate fit. The Widely Applicable Information Criterion (WAIC) was used to guide final model selection (Watanabe 2010). Using this model, we estimate occupancy probability for each species in different land use types. Only estimates for species with at least 25 detections are included to avoid inference from limited data (resulting in 7 species being included in this analysis).

We drew posterior samples from the most parsimonious Bayesian occupancy model incorporating spatial autocorrelation to estimate the probability of occurrence of a species within a trapping grid cell (Supplementary Table 1). The most parsimonious model included variables for land use type and study village (Equation 9) to model the probability of occurrence. Equation 9 was used for the probability of detection component with a single latent spatial factor used.

$$\text{Probability of occurrence} \sim \text{Land use type} + \text{Village}$$

(Equation 9)

Co-occurrence of *Mastomys natalensis* with sympatric species

To investigate the potential for competitive exclusion of Mastomys natalensis, the reservoir host of LASV, by other sympatric species, we examined correlations in the predicted probabilities of occupancy between species pairs. These probabilities were derived for each grid cell from the spatial multi-species occupancy model. Analyses were stratified by land use type, and the Spearman rank correlation coefficient (ρ) was calculated for each species pair. A two-sided test for statistical significance was performed, with the null hypothesis being no correlation in the probabilities of occupancy for species pairs.

To minimise inference from sparse data, this analysis was restricted to species pairs that were detected in the observed data within the specific land use type being examined. Additionally, given the multiple statistical tests performed, we adopted a conservative threshold for statistical significance ($p \leq 0.0005$) to reduce the likelihood of reporting false-positive associations (Benjamin et al. 2018).

Statistically significant correlations were interpreted as indicating that one species was either more likely (positive correlation) or less likely (negative correlation) to occupy a grid cell within a given land use type when the other species was present. However, this analysis does not allow for inferences regarding the causal mechanism or directionality of any observed relationships (e.g., whether one species excludes or is excluded by another).

Results

Small-mammal detection and species community structure

Over the study period 684 individual small mammals were detected from 43,266 trap-nights across the four village study sites, yielding an overall trap success (TS) of 1.6%. The agricultural areas had the highest species richness and Shannon diversity values, while TS was greatest in village settings, including both inside and outside permanent structures (Table 1). Among the study sites, Seilama had the highest overall TS, species richness, and Shannon diversity. Notably, Seilama also exhibited the greatest TS within agricultural areas, unlike the other three sites. Species richness in Seilama was twice that of Lambayama, the peri-urban village study site, which also had the lowest species richness and Shannon diversity. In Lambayama, most rodents were detected within built-up village areas, reflecting its proximity to Kenema city.

Table 1. The number of trapped individuals (N), the number of trap nights (TN), trap-success (TS %), species richness and Shannon diversity by village and land use type.

Village	Land use	N	TN (TS %)	Species richness	Shannon diversity
All villages					
	Village	261	11516 (2.3%)	12	1.67
	Agriculture	379	26400 (1.4%)	17	2.20
	Forest	44	5350 (0.8%)	10	1.78
Baiama					
	Village	73	2716 (2.7%)	8	1.11
	Agriculture	45	4696 (1%)	9	1.96
	Forest	3	1568 (0.2%)	2	0.64
	Total	121	8980 (1.3%)	12	1.73
Lalehun					
	Village	54	2824 (1.9%)	9	1.65
	Agriculture	98	7608 (1.3%)	13	2.18
	Forest	5	1862 (0.3%)	3	1.05
	Total	157	12294 (1.3%)	13	2.21
Lambayama					
	Village	93	2736 (3.4%)	4	0.42
	Agriculture	50	6260 (0.8%)	6	1.19
	Total	143	8996 (1.6%)	6	1.03
Seilama					
	Village	41	3240 (1.3%)	8	1.54
	Agriculture	186	7836 (2.4%)	13	1.97
	Forest	36	1920 (1.9%)	8	1.51
	Total	263	12996 (2%)	14	2.07

The most commonly detected rodent species across all land use types was *M. natalensis* (N = 113, 16.5%), followed by *Praomys rostratus* (N = 102, 14.9%), *M. musculus* (N = 90, 13.2%), *R. rattus* (N = 88, 12.9%) and *Lophuromys sikapusi* (N = 57, 8.3%) and *Mus setulosus* (N = 43, 6.3%). Among non-rodent species, the insectivorous shrew *Crocidura olivieri* was the most frequently detected (N = 105, 15.4%). *Mastomys natalensis* and *R. rattus* were found in all village study sites, although *M. natalensis* was absent in forest settings (Figure 2). The invasive rodent *M. musculus* was detected only in Lambayama, the peri-urban site.

Detection rates (number of individuals per 1,000 trap-nights) varied significantly by species, land use type, and village study site. The highest detection rate was observed for *M. musculus* in the Lambayama village site, while *M. natalensis* and *R. rattus* showed high detection rates across multiple sites in village land use types. In contrast, *P. rostratus* had the highest detection rates in forest and agricultural areas.

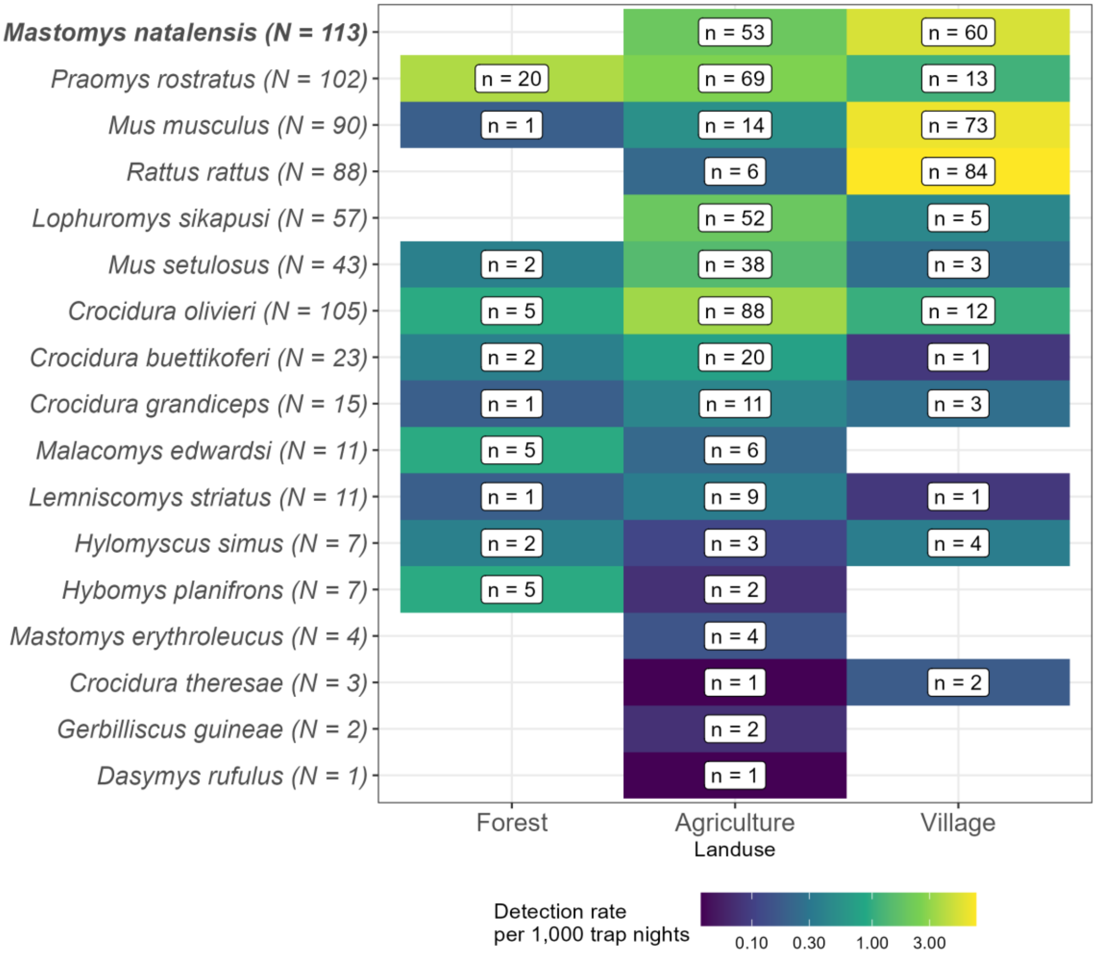

Figure 2. *Detection rate per 1,000 trap nights of small mammal species across different land use types (grouped across village study sites). The total number of detections in this study is shown next to the species binomial name (N). The number of detections of each species in each land use is shown in the label (n). The colour of the tile corresponds to the detection rate per 1,000 trap nights.*

Seasonal variation in species detection was observed but did not show consistent trends across all species. While *M. musculus* had higher detection rates during the rainy season, species such as *L. sikapusi* and *Mus setulosus* were more frequently detected in the dry season. For most other species, detection rates were similar across seasons (Supplementary Figure 5A). When stratified by land use type, some variations were evident. For instance, *M. natalensis* was more frequently detected in village settings than in agricultural areas during the rainy season, but detection rates were similar between the two land use types in the dry season. *Praomys rostratus* showed higher detection rates in forests during the dry season compared with the rainy season. No other species showed notable seasonal variations when stratified by land use type (Supplementary Figure 5B).

Estimating the effect of land use on species occurrence and richness

We found three patterns of probability of occurrence (ψ) within a trapping grid cell for the seven included species (Figure 3 and, marginal effects of the detection parameters are shown in Supplementary Figures 6-8). First, *M. natalensis*, *R. rattus* and *M. musculus* had greatest probabilities of occurrence in villages with lower occurrence probabilities in agricultural and forest areas. *Mastomys natalensis* differed from the two commensal, invasive species (*R. rattus* and *M. musculus*) as their probability of occurrence in agricultural settings, while lower than village settings, remained generally high. Second, *P. rostratus* had high probability of occurrence in forests with lower probabilities in agricultural areas and villages. Finally, *C. olivieri*, *L. sikapusi* and *M. setulosus* had their highest probabilities of occurrence in agricultural areas with lower probabilities of occurrence in forests and villages. No species showed high probability of occurrence across all land use types, consistent with species being adapted to distinct ecological niches.

The probability of occurrence within a trapping grid cell, within the same land use type showed wide variability for some species. For example, the narrow range of probabilities for *M. natalensis* in forests (0-13%) is suggestive that the probability of this species occurring within forests is low. This compares to the wide variability for *P. rostratus* in agricultural areas (0-90%), this suggests that additional environmental factors beyond land use type are affecting the probability occurrence.

To further explore this, we stratified village study sites by human population density into rural and peri-urban sites (rural <= 500 individuals per 1km^2) (Figure 3). The probability of occurrence of *M. natalensis* was importantly different between these settings, with high probability of occurrence in both agricultural and village settings in rural areas but substantially lower probability in peri-urban study sites. The same pattern was observed for *R. rattus*. For the rodent species predicted to have a lower probability of occurrence in village settings (*P. rostratus*, *L. sikapusi* and *M. setulosus*) probabilities of occurrence were greater in all land use types in rural areas compared to peri-urban areas. Shrew species had similar probabilities of occurrence in rural and peri-urban areas. Human population density itself or other environmental factors strongly associated with human population density may therefore be importantly contributing to small-mammal species occurrence.

In contrast to species found throughout our study area, *M. musculus* was predicted to have a low probability of occurrence in all land use types in rural areas, with high probabilities of occurrence only for village settings in peri-urban areas. The occurrence probabilities for the three commensal species (*M. natalensis*, *R. rattus* and *M. musculus*) suggest that competition may be a factor in reducing the occurrence probabilities of *M. natalensis* and *R. rattus* in the presence of *M. musculus* as in its absence these two species have high occurrence probabilities in villages.

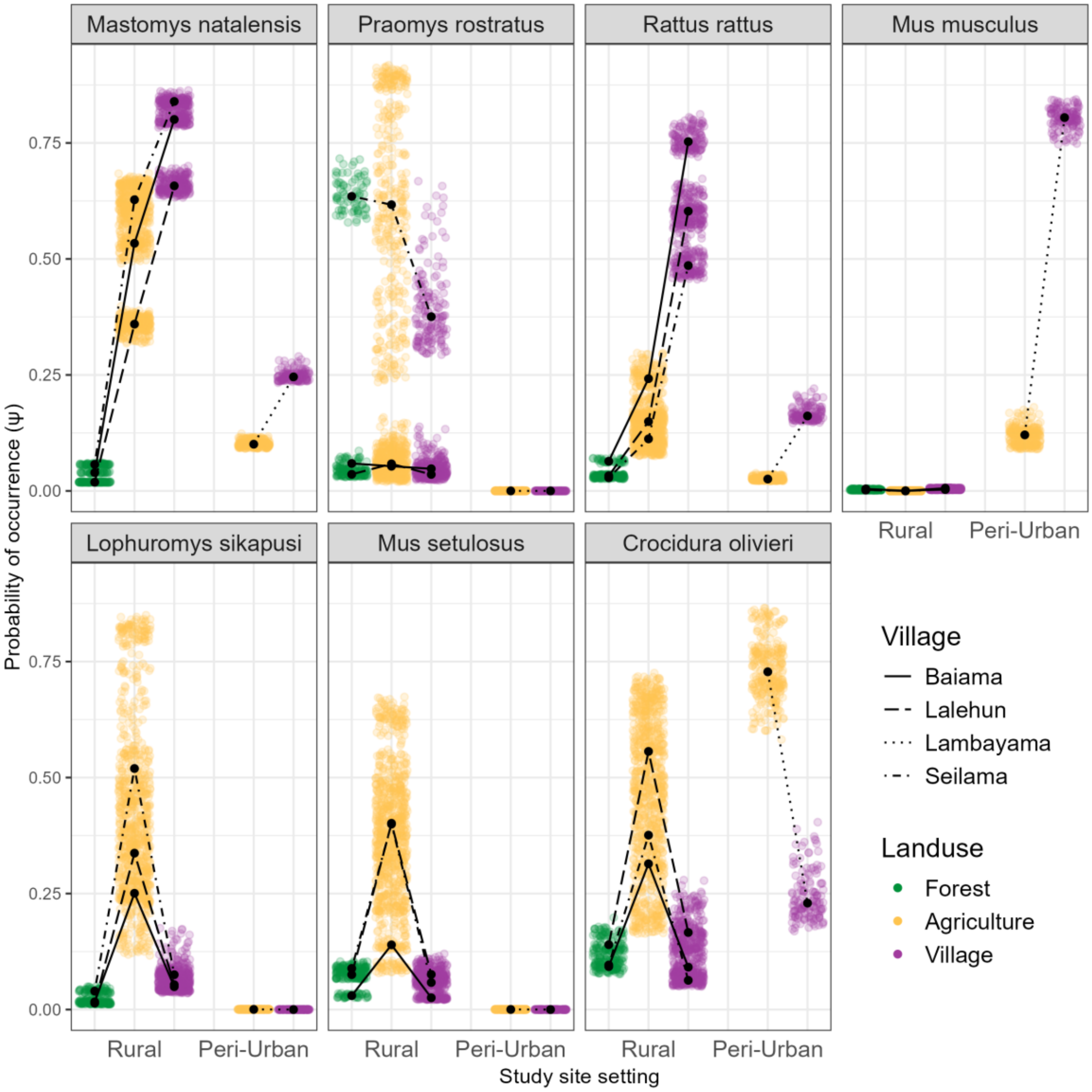

Figure 3. *Probability of species occurrence (ψ) across a land use gradient, stratified by rural and peri-urban village study sites, for the seven rodent and shrew species. Each coloured point represents the median predicted probability of occurrence for a species, obtained from the posterior distribution at each trapping grid cell. Colours correspond to different land use types. Predictions are based on 2,068 trapping grid cells. Black points indicate the median probability of occurrence within each land use type, grouped by village, with lines connecting estimates within villages for different land use types. Lines are shown only to link the occupancy estimates for each land use type within a given village.*

These patterns of species occurrence, particularly in relation to human population density and land use type, suggest that urbanisation and land use change could substantially influence the distribution of small-mammal species, with potential implications for zoonotic disease dynamics and biodiversity conservation.

Co-occurrence of species within land use types

The tests for species correlations reveal patterns consistent with our original hypothesis that the local spatial distribution of *M. natalensis* is regulated by biotic interactions with co-occurring species (Figure 4). While this analytical approach cannot demonstrate causality between co-occurrence and the probability of occurrence, it is possible that unmeasured factors are influencing the observed associations. In land use types where both *M. natalensis* and *M. musculus* co-occurred, the presence of one species was associated with a reduced probability of occurrence for the other. Statistically significant negative correlations were observed in agricultural (Spearman's $\rho = -0.67$, $p < 0.0001$) and village ($\rho = -0.35$, $p < 0.0001$) settings. In contrast, a positive correlation was found between the occurrences of *M. natalensis* and the other commensal, invasive rodent *R. rattus*, with significant positive correlations in both agricultural ($\rho = 0.51$, $p < 0.0001$) and village ($\rho = 0.36$, $p < 0.0001$) settings.

Within villages, high probabilities of *M. musculus* presence were associated with lower probabilities for all other rodent species. This pattern was not replicated for *M. natalensis* and *R. rattus*, which were positively correlated with the co-occurrence of native rodent species, including *P. rostratus*, *L. sikapusi*, and *M. setulosus*. Across all land use types, the presence of the shrew species, *C. olivieri* was negatively correlated with the presence of rodent species.

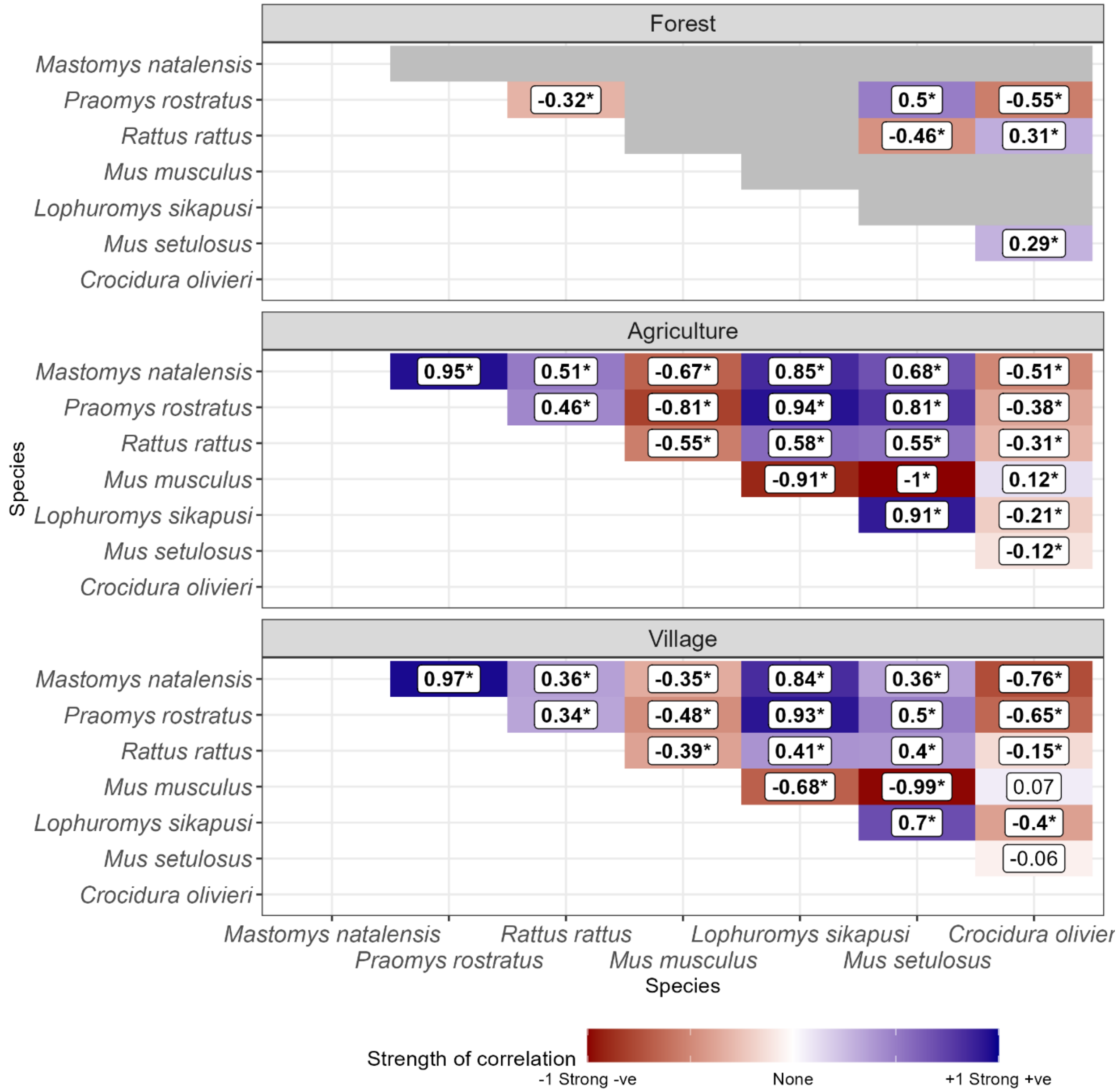

Figure 4. *Spearman's rank correlations for the modelled site-level probability of occurrence of species pairs in different land use types. Positive values (blue shades) represent positive correlation coefficients between the occurrence of two species. Negative values (red shades) represent negative correlation between the occurrence of two species. Numbers in bold typeface and indicated with an asterisk (*) are statistically significant at a level of p <= 0.0005. Grey tiles are used where no detections of the species pair in the land use type were observed and therefore excluded from analysis.*

Discussion

This study provides valuable insights into the dynamics of small-mammal communities in a Lassa fever endemic region of Eastern Sierra Leone, focusing on how land-use types influence species richness, diversity, and the risk of viral spillover. Our results indicate that species richness and diversity were highest in agricultural settings, followed by villages, with lower richness in forests. Agricultural habitats support both synanthropic and non-synanthropic species, increasing the potential for viral sharing.

The highest probability of occupancy for the LASV reservoir host, *M. natalensis*, was observed in villages and agricultural settings, while it was likely absent from forests. This pattern mirrors that of the invasive commensal species *M. musculus* and *R. rattus*, suggesting that human-modified landscapes may be key drivers of rodent distribution. Stratification by human population density revealed that *M. natalensis* occupancy was lower in peri-urban settings, where *M. musculus* dominates. Importantly, we identified a negative correlation in the probability of co-occurrence between *M. natalensis* and *M. musculus* within villages, which could have important implications for understanding observed Lassa fever outbreaks.

Our study suggests that agricultural settings, with their higher species richness, may be hotspots for LASV transmission among rodents. The diverse rodent communities found in these areas could facilitate viral persistence and reintroduction, particularly among isolated populations of *M. natalensis*. These findings underscore the importance of considering both species diversity and land use when assessing the risk of zoonotic spillover.

Small-mammal communities are associated with land use type

Small-mammal species richness was greatest in agricultural settings. In these settings both synanthropic and non-synanthropic species were found. The higher species richness in agricultural environments provides more opportunities for cross-species transmission of LASV within diverse small-mammal communities.

Evidence suggests that the wider species community may play a role in LASV transmission. Current or prior infection with LASV (through detection of virus or antibodies), has been identified in 11 additional small-mammal species to *M. natalensis*. Whether these infections are incidental or represent competent chains of viral transmission remains unclear (Monath et al. 1974; Demby et al. 2001; Fichet-Calvet et al. 2014; Olayemi et al. 2016; Simons et al. 2023). It is possible that viral sharing within small-mammal communities is greatest in the more species rich agricultural settings, allowing introduction or re-introduction of LASV into isolated commensal species populations following local extinction of virus (Bordes, Blasdell, and Morand 2015). This may be particularly important for maintaining viral persistence through time in spatially isolated *M. natalensis* populations, where rapid depletion of susceptible individuals is expected in well-mixed populations (Goyens et al. 2013). Our findings, along with previous studies, show that *M. natalensis* is absent from forested regions and populations are spatially isolated, further supporting the hypothesis of limited geographic dispersal of this species

(Leirs, Verheyen, and Verhagen 1996; Denys et al. 2005; Mariën et al. 2018). However, the role of the wider rodent community in facilitating LASV transmission between isolated *M. natalensis* populations warrants further investigation.

Although previous studies from Guinea and Sierra Leone have reported seasonal fluctuations in *M. natalensis* prevalence, our findings of similar or increased prevalence during the dry season suggest that localized factors such as agricultural practices or food storage, may influence rodent behaviour in this region somewhat differently than previously documented (Fichet-Calvet et al. 2007; Bangura et al. 2021). Alternatively, increased trap-shyness during periods of increased abundance may mask replication of previous findings. Further studies on small-mammal communities, incorporating local human community behaviour and practices, conducted over longer time periods and across different geographic regions, would be valuable in identifying how seasonal habitat preferences of these rodents vary (Kelly et al. 2013; Leach et al. 2017). These findings underscore the importance of considering local human activities, such as food storage and agricultural practices (e.g., one vs. two annual planting and harvesting cycles), when modelling seasonal patterns in rodent behaviour. Such practices may alter rodent abundance and movement in ways that differ from areas where *M. natalensis* displays more predictable seasonal patterns due to other environmental or ecological factors.

The prevalence of *M. natalensis* within households has been suggested as a key driver of Lassa fever outbreaks, likely due to increased human-rodent contact in household settings (Bonwitt et al. 2017; Mariën et al. 2020). Therefore, the movement of *M. natalensis* from species-rich agricultural areas to households may play a critical role in the transmission dynamics of LASV. Understanding these movement patterns and their interactions with local human activities will be essential for developing targeted interventions to reduce the risk of Lassa fever outbreaks.

Evidence for biotic interactions shaping patterns of small-mammal species diversity

The segregation of small-mammal species into distinct ecological niches, categorised by human-dominated (village and agricultural) or non-human-dominated (forest) land use types, underscores the significant role of biotic factors in species distribution. Our findings show a high predicted occupancy of both *M. natalensis* and *R. rattus* in human-dominated landscapes, with a positive correlation in their co-occurrence, aligning with a similar study conducted in another region of Sierra Leone (Bangura et al. 2021). In contrast, a study combining data from Guinea and Sierra Leone reported a decreased abundance (measured as catch per trap) of *M. natalensis* in the presence of *R. rattus* (Eskew et al. 2024). This suggests that *M. natalensis* may be displaced by *R. rattus* at a lower rate compared to M. musculus, but the extent of this displacement likely depends on which invasive species has already established dominance in a given area. Further evidence from Senegal suggests that *M. musculus* and *R. rattus* may invade along different routes (Dalecky et al. 2015). Therefore, the findings from this study and the Eskew study likely reflect a more intricate process of invasion and species displacement, which is contingent on the timing and dominance of either *M. musculus* or *R. rattus* within a landscape.

In village environments, the probability of *M. musculus* occurrence was negatively correlated with the co-occurrence of both *M. natalensis* and *R. rattus*. Interestingly, *M. musculus* was absent from rural villages where *R. rattus* and *M. natalensis* had high probabilities of occurrence. This pattern extended across all other rodent species in village environments, suggesting that *M. musculus* may be currently unable to establish populations in areas already dominated by *R. rattus* and *M. natalensis*. While it is not possible from this study to determine whether *M. musculus* is actively expanding into rural settings, the potential implications for small-mammal community dynamics and LASV transmission remain a critical area for future research.

To better understand the causal processes behind changes in small-mammal community structures, especially in response to the expansion of invasive species, long-term monitoring of rodent populations is necessary. Similar efforts conducted in Senegal would be valuable for tracking the progression of invasive species and their effects on local biodiversity and disease transmission risks (Dalecky et al. 2015).

Benefits and challenges of systematic small-mammal community sampling

Systematic investigation of small-mammal communities entails a greater sampling effort than targeted sampling of specific species in selected habitats. In this study, the overall TS was relatively low compared to other studies focusing on synanthropic rodent species (Olayemi et al. 2018; Bangura et al. 2021; Happi et al. 2022). Our TS rate of 3.3% within villages aligns with the 3% reported in Bo, Sierra Leone, but is notably lower than the 17%

and 14% reported in Nigeria and Guinea, respectively (Fichet-Calvet et al. 2007; Happi et al. 2022). This discrepancy may arise from differences in trapping methodologies, including the size of traps, trap locations, or the behaviour of target species. For example, *M. natalensis* captures in its Western range (Nigeria, Guinea, Sierra Leone) were less frequent than those observed in Tanzania, where TS rates of around 24% were reported in agricultural settings (Mulungu et al. 2013). One potential explanation is that the food availability in each setting might affect the species' behaviour, with environmental food sources influencing trap-shyness (Taylor, Hammond, and Quy 1974; Stryjek, Kalinowski, and Parsons 2019).

Despite the higher sampling effort required, systematic small-mammal community sampling offers distinct advantages over targeted species sampling, particularly in addressing biases related to species representation and pathogen detection. By adopting a broader, more inclusive approach, this method reduces the risk of overlooking less common species that may act as pathogen hosts but would otherwise be underrepresented in more focused sampling. Furthermore, this comprehensive approach provides greater insight into biotic interactions between species. While targeted sampling may focus on a single species or a small subset of species, a more systematic approach enables the detection of interactions among different rodent species, which may be crucial for understanding pathogen dynamics. For instance, our sampling design allowed us to observe interactions between synanthropic species like *M. musculus* and native species, potentially influencing pathogen transmission patterns. Wider sampling can reveal such interactions that might otherwise remain hidden, offering a more holistic view of the ecological factors contributing to pathogen spread and spillover risk.

Comparison between studies using different sampling techniques and study designs presents several challenges. Previous studies on rodent communities in the Lassa fever endemic region have used TS rates as an indirect measure of rodent abundance in the absence of capture-mark-recapture studies (Fichet-Calvet et al. 2009; Olayemi et al. 2018; Bangura et al. 2021). Our analysis, incorporating a model of imperfect detection, suggests estimating abundance from TS may not be applicable across different land use types and species (Supplementary Figure 8). For example, we observed that the probability of detecting *M. musculus* and *R. rattus* was higher than for native species when a consistent amount of trapping effort was applied. This finding aligns with previous research showing that detection rates, when used as a proxy for relative abundance, may be unreliable, especially when combining live-trapping and camera-trapping methods (Parsons, Clark, and Kays 2022). Several factors can contribute to variability in detection, including trap-shyness (neophobia) in non-synanthropic species, local resource availability, and trap placement (Stryjek, Kalinowski, and Parsons 2019). Understanding how these factors affect detection rates is essential for improving our ability to assess small-mammal populations accurately. Therefore, improving harmonisation of rodent sampling designs — particularly those incorporating systematic small-mammal community sampling — could enhance direct comparisons of species communities and pathogen prevalence across the Lassa fever endemic region (Simons et al. 2023). More broadly, this could lead to a deeper understanding of how different land use types and ecological factors influence rodent populations and their role in pathogen transmission.

There are several limitations to the current study. One limitation is the relatively short duration of our animal sampling (less than three years). Given that rodent populations can fluctuate significantly over longer time periods, it is possible that important variations in abundance were missed during our study. As a result, the probability of occurrence for certain species may have been underestimated, particularly for species that were at low abundance during our survey period. Extending the sampling period would help to better capture temporal changes in species occurrence and abundance. Additionally, land use in Sierra Leone, particularly in agricultural areas, follows multi-year cycles of cultivation, fallow, and reconversion to cultivated land. To more comprehensively understand the effects of land use change on rodent communities, it would be useful to focus on a single location that spans the transition from forested land to agricultural, fallow, and degraded forest land use. Such a study would provide insights into how these different land management practices influence rodent community dynamics and pathogen risk. Furthermore, unobserved characteristics of the villages in our study may have contributed to variations in the composition of rodent communities, as suggested by the wide posterior distributions for some species. Expanding our study to include a greater number of villages would help increase the generalisability of our findings and improve the robustness of conclusions drawn for the wider region.

Implications for understanding the risk of LASV spillover

The lower occurrence of *M. natalensis* in agricultural and forest land use is consistent with growing evidence of LASV prevalence heterogeneity across the endemic region (Mariën et al. 2020). In some village communities, no current evidence of LASV transmission has been detected within rodent populations, despite prior human cases or serological evidence of outbreaks. This suggests that pathogen prevalence in rodents may vary significantly over time and space (Bangura et al. 2021; McCormick et al. 1987; Leski et al. 2015). As discussed earlier, LASV transmission among the rodent community may be short-lived, with rapid local extinction of the virus (Goyens et al. 2013). These dynamics raise the possibility that non-*M. natalensis* species may play a crucial role in transferring the virus between communities of *M. natalensis* that reside in villages separated by forest or other land use types that are not colonised by *M. natalensis*, leading to pathogen re-introduction. Species found in forested settings, such as *P. rostratus*, *M. setulosus*, *Malacomys edwardsi*, and *L. striatus*, have shown evidence of prior LASV exposure, as indicated by antibodies (Monath et al. 1974; Demby et al. 2001; Fichet-Calvet et al. 2014; Olayemi et al. 2016; Simons et al. 2023). To better understand the temporal and spatial variability in LASV prevalence, it is imperative to conduct small-mammal sampling and movement ecology studies across the broader land use gradient.

Current disease models of LASV risk largely fail to incorporate the role of multiple rodent species and the potential biotic interactions between them (Basinski et al. 2021; Mylne et al. 2015; Olugasa et al. 2014; Redding et al. 2016; Fichet-Calvet and Rogers 2009; Klitting et al. 2022). Our findings, which highlight interactions between *M. natalensis* and primarily *M. musculus*, suggest that Lassa fever risk could potentially be reduced in areas where *M. musculus* is present. This raises the need for further research into the competence of *M. musculus* as a host for LASV, as previous serological evidence has shown exposure to the virus in this species (Demby et al. 2001). If *M. musculus* is not a competent host for LASV, this could help explain why Lassa fever is more commonly reported in rural areas of the endemic region, rather than urban centers, where *M. musculus* may have displaced more competent viral hosts. To test this hypothesis, further research systematically sampling along the urban-rural gradient is essential. Such work could significantly impact future projections of Lassa fever risk, especially given the rapid population growth and urbanisation occurring across West Africa. The expansion of *M. musculus* in these settings may moderate the risk of increased Lassa fever outbreaks, making it crucial to better understand the implications of urbanisation on zoonotic outbreak risks.

References

Agbonlahor, Dennis E., George O. Akpede, Christian T. Happi, and Oyewale Tomori. 2021. “52 Years of Lassa Fever Outbreaks in Nigeria, 1969–2020: An Epidemiologic Analysis of the Temporal and Spatial Trends.” *The American Journal of Tropical Medicine and Hygiene* -1 (August). https://doi.org/10.4269/ajtmh.20-1160.

Altschul, S. F., W. Gish, W. Miller, E. W. Myers, and D. J. Lipman. 1990. “Basic Local Alignment Search Tool.” *Journal of Molecular Biology* 215 (3): 403–10. https://doi.org/10.1016/S0022-2836(05)80360-2.

Arruda, Liã Bárbara, Najmul Haider, Ayodeji Olayemi, David Simons, Deborah Ehichioya, Adesola Yinka-Ogunleye, Rashid Ansumana, et al. 2021. “The Niche of One Health Approaches in Lassa Fever Surveillance and Control.” *Annals of Clinical Microbiology and Antimicrobials* 20 (1): 29. https://doi.org/10.1186/s12941-021-00431-0.

Bangura, Umaru, Jacob Buanie, Joyce Lamin, Christopher Davis, Gedeon Ngiala Bongo, Michael Dawson, Rashid Ansumana, et al. 2021. “Lassa Virus Circulation in Small

Mammal Populations in Bo District, Sierra Leone." *BIOLOGY-BASEL* 10 (1). https://doi.org/10.3390/biology10010028.

Basinski, Andrew J., Elisabeth Fichet-Calvet, Anna R. Sjodin, Tanner J. Varrelman, Christopher H. Remien, Nathan C. Layman, Brian H. Bird, et al. 2021. "Bridging the Gap: Using Reservoir Ecology and Human Serosurveys to Estimate Lassa Virus Spillover in West Africa." Edited by Amy Wesolowski. *PLOS Computational Biology* 17 (3): e1008811. https://doi.org/10.1371/journal.pcbi.1008811.

Benjamin, Daniel J., James O. Berger, Magnus Johannesson, Brian A. Nosek, E.-J. Wagenmakers, Richard Berk, Kenneth A. Bollen, et al. 2018. "Redefine Statistical Significance." *Nature Human Behaviour* 2 (1): 6–10. https://doi.org/10.1038/s41562-017-0189-z.

Bonner, Phillip Cullison, Wolf-Peter Schmidt, Steven R. Belmain, Babafemi Oshin, Debbie Baglole, and Matthias Borchert. 2007. "Poor Housing Quality Increases Risk of Rodent Infestation and Lassa Fever in Refugee Camps of Sierra Leone." *American Journal of Tropical Medicine & Hygiene* 77 (1): 169–75.

Bonwitt, Jesse, Almudena Mari Sáez, Joseph Lamin, Rashid Ansumana, Michael Dawson, Jacob Buanie, Joyce Lamin, et al. 2017. "At Home with Mastomys and Rattus: Human-Rodent Interactions and Potential for Primary Transmission of Lassa Virus in Domestic Spaces." *The American Journal of Tropical Medicine and Hygiene* 96 (4): 935–43. https://doi.org/10.4269/ajtmh.16-0675.

Bordes, Frédéric, Kim Blasdell, and Serge Morand. 2015. "Transmission Ecology of Rodent-Borne Diseases: New Frontiers." *Integrative Zoology* 10 (5): 424–35. https://doi.org/10.1111/1749-4877.12149.

Carlson, Colin J., Cole B. Brookson, Daniel J. Becker, Caroline A. Cummings, Rory Gibb, Fletcher W. Halliday, Alexis M. Heckley, et al. 2025. "Pathogens and Planetary Change." *Nature Reviews Biodiversity* 1 (1): 32–49. https://doi.org/10.1038/s44358-024-00005-w.

Cuypers, Laura N, Wim L Cuypers, Amélie Gildemyn-Blomme, Laura Abraham, Senne Aertbeliën, Apia W Massawe, Benny Borremans, Sophie Gryseels, and Herwig Leirs. 2017. "No Evidence for Avoidance of Black Rat Scent by the Presumably Less Competitive Natal Multimammate Mouse in a Choice Experiment." *African Zoology* 52 (2): 119–23. https://doi.org/10.1080/15627020.2017.1307139.

Dalecky, Ambroise, Khalilou Ba, Sylvain Piry, Cedric Lippens, Christophe A. Diagne, Mamadou Kane, Aliou Sow, et al. 2015. "Range Expansion of the Invasive House Mouse Mus Musculus Domesticus in Senegal, West Africa: A Synthesis of Trapping Data over Three Decades, 1983-2014." *Mammal Review* 45 (3): 176–90. https://doi.org/10.1111/mam.12043.

Demby, Austin H., Alphonse Inapogui, Kandeh Kargbo, James Koninga, Kerfalla Kourouma, James Kanu, Mamadi Coulibaly, et al. 2001. "Lassa Fever in Guinea: II. Distribution and

Prevalence of Lassa Virus Infection in Small Mammals." *Vector-Borne and Zoonotic Diseases* 1 (4): 283–97. https://doi.org/10.1089/15303660160025912.

Denys, C., E. Lecompte, E. Calvet, M. D. Camara, A. Doré, K. Koulémou, F. Kourouma, et al. 2005. "Community Analysis of Muridae (Mammalia, Rodentia) Diversity in Guinea: A Special Emphasis on Mastomys Species and Lassa Fever Distributions." In *African Biodiversity*, by Bernhard A. Huber, Bradley J. Sinclair, and Karl-Heinz Lampe, 339–50. Boston, MA: Springer US. https://doi.org/10.1007/0-387-24320-8_34.

Doser, Jeffrey W., Andrew O. Finley, Marc Kéry, and Elise F. Zipkin. 2022. "spOccupancy: An r Package for Single-Species, Multi-Species, and Integrated Spatial Occupancy Models." *Methods in Ecology and Evolution*. https://doi.org/10.1111/2041-210X.13897.

Ecke, Frauke, Barbara A. Han, Birger Hörnfeldt, Hussein Khalil, Magnus Magnusson, Navinder J. Singh, and Richard S. Ostfeld. 2022. "Population Fluctuations and Synanthropy Explain Transmission Risk in Rodent-Borne Zoonoses." *Nature Communications* 13 (1): 7532. https://doi.org/10.1038/s41467-022-35273-7.

Eskew, Evan A., Brian H. Bird, Bruno M. Ghersi, James Bangura, Andrew J. Basinski, Emmanuel Amara, Mohamed A. Bah, et al. 2024. "Reservoir Displacement by an Invasive Rodent Reduces Lassa Virus Zoonotic Spillover Risk." *Nature Communications* 15 (1): 3589. https://doi.org/10.1038/s41467-024-47991-1.

Fichet-Calvet, Elisabeth. 2014. "Chapter 5 - Lassa Fever: A Rodent-Human Interaction." In *The Role of Animals in Emerging Viral Diseases*, edited by Nicholas Johnson, 89–123. Boston: Academic Press. https://doi.org/10.1016/B978-0-12-405191-1.00005-3.

Fichet-Calvet, Elisabeth, Beate Becker-Ziaja, Lamine Koivogui, and Stephan Gunther. 2014. "Lassa Serology in Natural Populations of Rodents and Horizontal Transmission." *Vector Borne & Zoonotic Diseases* 14 (9): 665–74. https://doi.org/10.1089/vbz.2013.1484.

Fichet-Calvet, Elisabeth, Kekoura Koulemou, Lamine Koivogui, Barre Soropogui, Oumar Sylla, Emilie Lecompte, Stephane Daffis, et al. 2005. "Spatial Distribution of Commensal Rodents in Regions with High and Low Lassa Fever Prevalence in Guinea." *Belgian Journal of Zoology* 135 (December): 63–67. https://biblio.naturalsciences.be/associated_publications/bjz/bibliographic-references/ISI_000203706900011.

Fichet-Calvet, Elisabeth, Emilie Lecompte, Lamine Koivogui, Barré Soropogui, Amadou Doré, Fodé Kourouma, Oumar Sylla, Stéphane Daffis, Kékoura Koulémou, and Jan Ter Meulen. 2007. "Fluctuation of Abundance and Lassa Virus Prevalence in Mastomys Natalensis in Guinea, West Africa." *Vector Borne and Zoonotic Diseases* 7 (2): 119–28. https://doi.org/10.1089/vbz.2006.0520.

Fichet-Calvet, Elisabeth, Emilie Lecompte, Frederic Veyrunes, Patrick Barrière, Violaine Nicolas, and Kékoura Koulémou. 2009. "Diversity and Dynamics in a Community of Small

Mammals in Coastal Guinea, West Africa." *Belgian Journal of Zoology* 139 (2): 93–102. http://www.vliz.be/nl/open-marien-archief?module=ref&refid=204614.

Fichet-Calvet, Elisabeth, and David John Rogers. 2009. "Risk Maps of Lassa Fever in West Africa." *PLOS Neglected Tropical Diseases* 3 (3): e388. https://doi.org/10.1371/journal.pntd.0000388.

Database of Global Administrative Areas. GADM [Internet]. 2022 [retreived 2021 Apr 25]. Available from: https://gadm.org/index.html

Garba, Madougou, Ambroise Dalecky, Ibrahima Kadaoure, Mamadou Kane, Karmadine Hima, Sophie Veran, Sama Gagare, et al. 2014. "Spatial Segregation Between Invasive and Native Commensal Rodents in an Urban Environment: A Case Study in Niamey, Niger." *PLOS ONE* 9 (11): e110666. https://doi.org/10.1371/journal.pone.0110666.

Gibb, Rory, Lina M. Moses, David W. Redding, and Kate E. Jones. 2017. "Understanding the Cryptic Nature of Lassa Fever in West Africa." *Pathogens and Global Health* 111 (6): 276–88. https://doi.org/10.1080/20477724.2017.1369643.

Gibb, Rory, David W. Redding, Kai Qing Chin, Christl A. Donnelly, Tim M. Blackburn, Tim Newbold, and Kate E. Jones. 2020. "Zoonotic Host Diversity Increases in Human-Dominated Ecosystems." *Nature* 584 (7821): 398–402. https://doi.org/10.1038/s41586-020-2562-8.

Gibb, Rory, David W. Redding, Sagan Friant, and Kate E. Jones. 2025. "Towards a 'People and Nature' Paradigm for Biodiversity and Infectious Disease." *Philosophical Transactions of the Royal Society B: Biological Sciences* 380 (1917): 20230259. https://doi.org/10.1098/rstb.2023.0259.

Glidden, Caroline K., Nicole Nova, Morgan P. Kain, Katherine M. Lagerstrom, Eloise B. Skinner, Lisa Mandle, Susanne H. Sokolow, et al. 2021. "Human-Mediated Impacts on Biodiversity and the Consequences for Zoonotic Disease Spillover." *Current Biology* 31 (19): R1342–61. https://doi.org/10.1016/j.cub.2021.08.070.

Goyens, J., J. Reijniers, B. Borremans, and H. Leirs. 2013. "Density Thresholds for Mopeia Virus Invasion and Persistence in Its Host Mastomys Natalensis." *Journal of Theoretical Biology* 317 (January): 55–61. https://doi.org/10.1016/j.jtbi.2012.09.039.

Grant, Donald S., Emily J. Engel, Nicole Roberts Yerkes, Lansana Kanneh, James Koninga, Michael A. Gbakie, Foday Alhasan, et al. 2023. "Seroprevalence of Anti-Lassa Virus IgG Antibodies in Three Districts of Sierra Leone: A Cross-Sectional, Population-Based Study." *PLOS Neglected Tropical Diseases* 17 (2): e0010938. https://doi.org/10.1371/journal.pntd.0010938.

Han, Barbara A., John Paul Schmidt, Sarah E. Bowden, and John M. Drake. 2015. "Rodent Reservoirs of Future Zoonotic Diseases." *Proceedings of the National Academy of Sciences* 112 (22): 7039–44. https://doi.org/10.1073/pnas.1501598112.

Happi, Anise N., Testimony J. Olumade, Olusola A. Ogunsanya, Ayotunde E. Sijuwola, Seto C. Ogunleye, Judith U. Oguzie, Cecilia Nwofoke, et al. 2022. “Increased Prevalence of Lassa Fever Virus-Positive Rodents and Diversity of Infected Species Found During Human Lassa Fever Epidemics in Nigeria.” *Microbiology Spectrum* 10 (4): e0036622. https://doi.org/10.1128/spectrum.00366-22.

Hima, Karmadine, Gualbert Houémenou, Sylvestre Badou, Madougou Garba, Henri-Joel Dossou, Jonas Etougbétché, Philippe Gauthier, et al. 2019. “Native and Invasive Small Mammals in Urban Habitats Along the Commercial Axis Connecting Benin and Niger, West Africa.” *Diversity* 11 (12): 238. https://doi.org/10.3390/d11120238.

IPBES. 2020. “Workshop Report on Biodiversity and Pandemics of the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES).” Zenodo. https://doi.org/10.5281/ZENODO.7432079.

IUCN. 2016. “The IUCN Red List of Threatened Species 2016: Mastomys Natalensis.” International Union for Conservation of Nature. https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T12868A22425266.en.

Keenlyside, R. A., J. B. McCormick, P. A. Webb, E. Smith, L. Elliott, and K. M. Johnson. 1983. “Case-Control Study of Mastomys Natalensis and Humans in Lassa Virus-Infected Households in Sierra Leone.” *American Journal of Tropical Medicine & Hygiene* 32 (4): 829–37.

Keesing, Felicia, and Richard S. Ostfeld. 2021. “Impacts of Biodiversity and Biodiversity Loss on Zoonotic Diseases.” *Proceedings of the National Academy of Sciences* 118 (17): e2023540118. https://doi.org/10.1073/pnas.2023540118.

———. 2024. “Emerging Patterns in Rodent-Borne Zoonotic Diseases.” *Science* 385 (6715): 1305–10. https://doi.org/10.1126/science.adq7993.

Kelly, J. Daniel, M. Bailor Barrie, Rachel A. Ross, Brian A. Temple, Lina M. Moses, and Daniel G. Bausch. 2013. “Housing Equity for Health Equity: A Rights-Based Approach to the Control of Lassa Fever in Post-War Sierra Leone.” *BMC International Health and Human Rights* 13 (January). https://doi.org/10.1186/1472-698X-13-2.

Kingdon, Jonathan, and David Happold. 2013. “Mammals of Africa” 4.

Klitting, Raphaelle, Liana E. Kafetzopoulou, Wim Thiery, Gytis Dudas, Sophie Gryseels, Anjali Kotamarthi, Bram Vrancken, et al. 2022. “Predicting the Evolution of the Lassa Virus Endemic Area and Population at Risk over the Next Decades.” *Nature Communications* 13 (1): 5596. https://doi.org/10.1038/s41467-022-33112-3.

Leach, Melissa, Bernard Bett, M. Said, Salome Bukachi, Rosemary Sang, Neil Anderson, Noreen Machila, et al. 2017. “Local Disease–Ecosystem–Livelihood Dynamics: Reflections from Comparative Case Studies in Africa.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 372 (1725): 20160163. https://doi.org/10.1098/rstb.2016.0163.

Leirs, Herwig, Nils Chr Stenseth, James D. Nichols, James E. Hines, Ron Verhagen, and Walter Verheyen. 1997. “Stochastic Seasonality and Nonlinear Density-Dependent Factors Regulate Population Size in an African Rodent.” *Nature* 389 (6647): 176–80. https://doi.org/10.1038/38271.

Leirs, Herwig, Ron Verhagen, and Walter Verheyen. 1993. “Productivity of Different Generations in a Population of Mastomys Natalensis Rats in Tanzania.” *Oikos* 68 (1): 53–60. https://doi.org/10.2307/3545308.

Leirs, Herwig, Ron Verhagen, Walter Verheyen, Patrick Mwanjabe, and Thomas Mbise. 1996. “Forecasting Rodent Outbreaks in Africa: An Ecological Basis for Mastomys Control in Tanzania.” *Journal of Applied Ecology* 33 (5): 937–43. https://doi.org/10.2307/2404675.

Leirs, H., W. Verheyen, and R. Verhagen. 1996. “Spatial Patterns in Mastomys Natalensis in Tanzania (Rodentia, Muridae).” *Mammalia* 60 (4): 545–56. https://doi.org/10.1515/mamm.1996.60.4.545.

Leski, Tomasz A, Michael G Stockelman, Lina M Moses, Matthew Park, David A Stenger, Rashid Ansumana, Daniel G Bausch, and Baochuan Lin. 2015. “Sequence Variability and Geographic Distribution of Lassa Virus, Sierra Leone.” *Emerging Infectious Diseases* 21 (4): 609–18. https://doi.org/10.3201/eid2104.141469.

Lippens, C., A. Estoup, M. K. Hima, A. Loiseau, C. Tatard, A. Dalecky, K. Ba, et al. 2017. “Genetic Structure and Invasion History of the House Mouse (Mus Musculus Domesticus) in Senegal, West Africa: A Legacy of Colonial and Contemporary Times.” *Heredity* 119 (2): 64–75. https://doi.org/10.1038/hdy.2017.18.

Mantyka-Pringle, Chrystal S., Piero Visconti, Moreno Di Marco, Tara G. Martin, Carlo Rondinini, and Jonathan R. Rhodes. 2015. “Climate Change Modifies Risk of Global Biodiversity Loss Due to Land-Cover Change.” *Biological Conservation* 187 (July): 103–11. https://doi.org/10.1016/j.biocon.2015.04.016.

Mariën, Joachim, Giovanni Lo Iacono, Toni Rieger, Nfaly Magassouba, Stephan Günther, and Elisabeth Fichet-Calvet. 2020. “Households as Hotspots of Lassa Fever? Assessing the Spatial Distribution of Lassa Virus-Infected Rodents in Rural Villages of Guinea.” *Emerging Microbes & Infections* 9 (1): 1055–64. https://doi.org/10.1080/22221751.2020.1766381.

Mariën, Joachim, Fodé Kourouma, N’Faly Magassouba, Herwig Leirs, and Elisabeth Fichet-Calvet. 2018. “Movement Patterns of Small Rodents in Lassa Fever-Endemic Villages in Guinea.” *EcoHealth* 15 (2): 348–59. https://doi.org/10.1007/s10393-018-1331-8.

McCormick, J B, P A Webb, J W Krebs, K M Johnson, and E S Smith. 1987. “A Prospective Study of the Epidemiology and Ecology of Lassa Fever.” *The Journal of Infectious Diseases* 155 (3): 437–44. https://doi.org/10.1093/infdis/155.3.437.

Mendoza, Hugo, André V. Rubio, Gabriel E. García-Peña, Gerardo Suzán, and Javier A. Simonetti. 2019. "Does Land-Use Change Increase the Abundance of Zoonotic Reservoirs? Rodents Say Yes." *European Journal of Wildlife Research* 66 (1): 6. https://doi.org/10.1007/s10344-019-1344-9.

Monadjem, Ara, Peter J. Taylor, Christiane Denys, and Fenton P. D. Cotterill. 2015. *Rodents of Sub-Saharan Africa: A Biogeographic and Taxonomic Synthesis*. Berlin, München, Boston: DE GRUYTER. https://doi.org/10.1515/9783110301915.

Monath, T. P., V. F. Newhouse, G. E. Kemp, H. W. Setzer, and A. Cacciapuoti. 1974. "Lassa Virus Isolation from Mastomys Natalensis Rodents During an Epidemic in Sierra Leone." *Science* 185 (4147): 263–65. https://doi.org/10.1126/science.185.4147.263.

Mulungu, Loth S, Victoria Ngowo, Mashaka Mdangi, Abdul S Katakweba, Protas Tesha, Furaha P Mrosso, Mary Mchomvu, Paul M Sheyo, and Bukhet S Kilonzo. 2013. "Population Dynamics and Breeding Patterns of Multimammate Mouse, Mastomys Natalensis (Smith 1834), in Irrigated Rice Fields in Eastern Tanzania." *Pest Management Science* 69 (3): 371–77. https://doi.org/10.1002/ps.3346.

Mylne, Adrian Q. N., David M. Pigott, Joshua Longbottom, Freya Shearer, Kirsten A. Duda, Jane P. Messina, Daniel J. Weiss, Catherine L. Moyes, Nick Golding, and Simon I. Hay. 2015. "Mapping the Zoonotic Niche of Lassa Fever in Africa." *Transactions of The Royal Society of Tropical Medicine and Hygiene* 109 (8): 483–92. https://doi.org/10.1093/trstmh/trv047.

Naeem, Shahid, J. Emmett Duffy, and Erika Zavaleta. 2012. "The Functions of Biological Diversity in an Age of Extinction." *Science* 336 (6087): 1401–6. https://doi.org/10.1126/science.1215855.

Newbold, Tim, Lawrence N. Hudson, Samantha L. L. Hill, Sara Contu, Igor Lysenko, Rebecca A. Senior, Luca Börger, et al. 2015. "Global Effects of Land Use on Local Terrestrial Biodiversity." *Nature* 520 (7545): 45–50. https://doi.org/10.1038/nature14324.

Oksanen, Jari, Gavin L. Simpson, F. Guillaume Blanchet, Roeland Kindt, Pierre Legendre, Peter R. Minchin, R. B. O'Hara, et al. 2022. *Vegan: Community Ecology Package*. https://CRAN.R-project.org/package=vegan.

Olayemi, Ayodeji, Daniel Cadar, N'Faly Magassouba, Adeoba Obadare, Fode Kourouma, Akinlabi Oyeyiola, Samuel Fasogbon, et al. 2016. "New Hosts of the Lassa Virus." *Scientific Reports* 6 (1): 25280. https://doi.org/10.1038/srep25280.

Olayemi, Ayodeji, Adeoba Obadare, Akinlabi Oyeyiola, Samuel Fasogbon, Joseph Igbokwe, Felix Igbahenah, Daniel Ortsega, Stephan Günther, Erik Verheyen, and Elisabeth Fichet-Calvet. 2018. "Small Mammal Diversity and Dynamics Within Nigeria, with Emphasis on Reservoirs of the Lassa Virus." *Systematics and Biodiversity* 16 (2): 118–27. https://doi.org/10.1080/14772000.2017.1358220.

Olugasa, Babasola O, John B Dogba, Bamidele Ogunro, Eugene A Odigie, Jomah Nykoi, Johnson F Ojo, Olalekan Taiwo, Abraham Kamara, Charles K Mulbah, and Ayotunde J Fasunla. 2014. "The Rubber Plantation Environment and Lassa Fever Epidemics in Liberia, 2008-2012: A Spatial Regression." *Spatial and Spatio-Temporal Epidemiology* 11 (101516571): 163–74. https://doi.org/10.1016/j.sste.2014.04.005.

Ostfeld, Richard S., and Robert D. Holt. 2004. "Are Predators Good for Your Health? Evaluating Evidence for Top-down Regulation of Zoonotic Disease Reservoirs." *Frontiers in Ecology and the Environment* 2 (1): 13–20. https://doi.org/10.1890/1540-9295(2004)002[0013:APGFYH]2.0.CO;2.

Parsons, Arielle W, James S Clark, and Roland Kays. 2022. "Monitoring Small Mammal Abundance Using NEON Data: Are Calibrated Indices Useful?" *Journal of Mammalogy*, November, gyac096. https://doi.org/10.1093/jmammal/gyac096.

Pebesma, Edzer. 2018. "Simple Features for r: Standardized Support for Spatial Vector Data." *The R Journal* 10 (1): 439–46. https://journal.r-project.org/archive/2018/RJ-2018-009/index.html.

Pei, Shan, Pengbo Yu, Jayna Raghwani, Yuxin Wang, Ziyan Liu, Yidan Li, Yanchao Cheng, et al. 2024. "Anthropogenic Land Consolidation Intensifies Zoonotic Host Diversity Loss and Disease Transmission in Human Habitats." *Nature Ecology & Evolution* 9 (1): 99–110. https://doi.org/10.1038/s41559-024-02570-x.

QIAGEN. 2023. "DNeasy Blood & Tissue Kits." January 20, 2023. https://www.qiagen.com/us/products/discovery-and-translational-research/dna-rna-purification/dna-purification/genomic-dna/dneasy-blood-and-tissue-kit.

R Core Team. 2021. "R: A Language and Environment for Statistical Computing." Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Redding, David W., Rory Gibb, Chioma C. Dan-Nwafor, Elsie A. Ilori, Rimamdeyati Usman Yashe, Saliu H. Oladele, Michael O. Amedu, et al. 2021. "Geographical Drivers and Climate-Linked Dynamics of Lassa Fever in Nigeria." *Nature Communications* 12 (1): 5759. https://doi.org/10.1038/s41467-021-25910-y.

Redding, David W., Lina M. Moses, Andrew A. Cunningham, James Wood, and Kate E. Jones. 2016. "Environmental-Mechanistic Modelling of the Impact of Global Change on Human Zoonotic Disease Emergence: A Case Study of Lassa Fever." *Methods in Ecology and Evolution* 7 (6): 646–55. https://doi.org/10.1111/2041-210X.12549.

Sala, Osvaldo E., F. Stuart Chapin, III, Juan J. Armesto, Eric Berlow, Janine Bloomfield, Rodolfo Dirzo, et al. 2000. "Global Biodiversity Scenarios for the Year 2100." *Science* 287 (5459): 1770–74. https://doi.org/10.1126/science.287.5459.1770.

Salkeld, Daniel J, Kerry A Padgett, and James Holland Jones. 2013. "A Meta-Analysis Suggesting That the Relationship Between Biodiversity and Risk of Zoonotic Pathogen

Transmission Is Idiosyncratic." *Ecology Letters* 16 (5): 679–86. https://doi.org/10.1111/ele.12101.

Shannon, C. E. 1948. "A Mathematical Theory of Communication." *Bell System Technical Journal* 27 (3): 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x.

Simons, David, Lauren A Attfield, Kate E Jones, Deborah Watson-Jones, and Richard Kock. 2023. "Rodent Trapping Studies as an Overlooked Information Source for Understanding Endemic and Novel Zoonotic Spillover." *PLOS Neglected Tropical Diseases* 17 (1): e0010772. https://doi.org/10.1371/journal.pntd.0010772.

Stryjek, Rafal, Artur Kalinowski, and Michael H. Parsons. 2019. "Unbiased Sampling for Rodents and Other Small Mammals: How to Overcome Neophobia Through Use of an Electronic-Triggered Live Trap—a Preliminary Test." *Frontiers in Ecology and Evolution* 7. https://doi.org/10.3389/fevo.2019.00011.

Taylor, K. D., L. E. Hammond, and R. J. Quy. 1974. "The Reactions of Common Rats to Four Types of Live-Capture Trap." *The Journal of Applied Ecology* 11 (2): 453. https://doi.org/10.2307/2402199.

Watanabe, Sumio. 2010. "Asymptotic Equivalence of Bayes Cross Validation and Widely Applicable Information Criterion in Singular Learning Theory." *J. Mach. Learn. Res.* 11 (December): 3571–94. https://doi.org/10.5555/1756006.1953045.

World Health Organisation. 2022. "Lassa Fever." 2022. https://www.who.int/health-topics/lassa-fever#tab=tab_1.

Young, Hillary S., Rodolfo Dirzo, Kristofer M. Helgen, Douglas J. McCauley, Sarah A. Billeter, Michael Y. Kosoy, Lynn M. Osikowicz, Daniel J. Salkeld, Truman P. Young, and Katharina Dittmar. 2014. "Declines in Large Wildlife Increase Landscape-Level Prevalence of Rodent-Borne Disease in Africa." *Proceedings of the National Academy of Sciences* 111 (19): 7036–41. https://doi.org/10.1073/pnas.1404958111.

Young, Hillary S., Douglas J. McCauley, Rodolfo Dirzo, Charles L. Nunn, Michael G. Campana, Bernard Agwanda, Erik R. Otarola-Castillo, et al. 2017. "Interacting Effects of Land Use and Climate on Rodent-Borne Pathogens in Central Kenya." *Philosophical Transactions of the Royal Society B: Biological Sciences* 372 (1722): 20160116. https://doi.org/10.1098/rstb.2016.0116.