Contact networks of small mammals elucidate *Lassa mammarenavirus* transmission routes.

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# Abstract

Lassa fever, caused by *Lassa mammarenavirus* (LASV), is a zoonotic infectious disease endemic in several West African countries. Human infection is caused by spillover from rodent hosts, the primary reservoir being *Mastomys natalensis*, a commensal rodent species. In addition to the primary reservoir a further 11 rodent and shrew species have been found to be acutely infected or to have evidence of prior infection with the virus. These species rich small mammal communities are structured along land use gradients which is expected to moderate the risk of Lassa fever disease spillover into human populations. Here, we use a rodent trapping study, conducted over 43,266 trap nights, detecting 684 individual rodents to reconstruct rodent contact networks within the Lassa fever endemic Eastern Province, Sierra Leone. We found that rodent communities were more connected within agricultural land use settings than within villages or forest. We also found an increased odds of intraspecific contact among *M. natalensis* within agricultural settings compared to villages. Our results suggest, that among small mammals, LASV transmission may occur at greater rates within species rich agricultural settings than within villages. Finally, we report a LASV seroprevalence of 3.3% among these small mammal communities with antibodies detected within 6 rodent and shrew species. Expanding rodent trapping to both village and agricultural land use settings may elucidate the rodent and shrew species that are important for the maintenance of viral populations and the risk of zoonotic spillover into human populations.

# Introduction

Lassa fever caused by *Lassa mammarenavirus* (LASV) is a rodent borne endemic zoonotic disease, estimated to cause 100,000-900,000 annual infections across West Africa (McCormick et al. 1987; Basinski et al. 2021). Cases are sporadically reported from the Lassa fever endemic countries of Guinea, Liberia and Sierra Leone (Jetoh et al. 2022; Shaffer et al. 2021; Bausch et al. 2001). Within Sierra Leone disease outbreaks are commonly undetected, consistent with findings of up to of disease occur more frequently than the rate at which they are reported, this is supported by a recent seroprevalence study with up to 80% seropositivity to LASV among human communities in regions of the country considered non-endemic (Grant et al. 2023). Human infections are caused by pathogen spillover from rodent hosts, with limited subsequent human-to-human transmission (Lo Iacono et al. 2015). Therefore, characterising the interactions within small mammal communities through which pathogen transmission occurs are vital to understanding LASV transmission in the endemic setting.

The primary host of LASV, *Mastomys natalensis* is a native, commensal rodent species, occuring throughout sub-Saharan Africa. Pathogen challenge studies conducted on captive *M. natalensis* colonies found that acute infection does not result in significantly altered rodent behaviour or cause clinical pathology. LASV is transmitted between infected and susceptible individuals at low infectious doses, consistent transmission events occurring through a superficial wound caused by direct contact from an infected conspecific or indirect contact through contaminated environmental exposure (Safronetz et al. 2022). Within the rodent host viral RNA is detectable 3 days post infection, peaking within 1 to 2 weeks and resolving within 40 days. RNA persistance is observed in *M. natalensis* testes beyond this 40 day period suggesting that prolonged sexually mediated transmission may exist. The dynamics of antibody responses in infected rodents are not currently known. Based on a similar arenavirus (Morogoro virus), seroconversion is expected to occur 7 days post infection, with detectable antibodies (IgG) remaining beyond the point where circulating RNA has declined (40 days post-infection) (Borremans et al. 2015). A recent study conducted in Bo district, Sierra Leone reported a 2.8% prevalence of LASV antibodies and a prevalence of LASV acute infection (using PCR) of 0.3% highlighting the challenges of detecting acute infection in these populations (Bangura et al. 2021).

While *M. natalensis* is considered the primary reservoir for LASV, 11 further rodent species have been identified to be acutely or previously infected with LASV in endemic regions (Monath et al. 1974; Fichet-Calvet et al. 2014; Olayemi et al. 2016; Simons et al. 2023). The contribution of these additional species to pathogen spillover into human populations, and viral transmission or maintenance among rodent communities is unknown. Direct and indirect contact between rodents in species rich environments may produce incidental infections of non-reservoir species which are subsequently detected through surveillance activities, despite having little impact on viral transmission or maintenance (Gilbert et al. 2013). Alternatively, these species may facilitate transfer of this pathogen across the landscape, linking geographically isolated *M. natalensis* populations and causing reintroduction of virus into populations of the reservoir species (Cardenas et al. 2022; Caron et al. 2015). It is therefore important to characterise rodent interactions within endemic settings, expanding investigations of pathogen prevalence and transmission to the entire rodent community rather than focussing on a single species’ population (Albery et al. 2021). In this study, we characterise these potential interactions as a network, which we refer to as rodent contact networks. The nodes of a network represent individual rodents and the potential interactions are represented as connections (or edges) between these rodents.

The composition of rodent contact networks in Lassa fever endemic regions has not been systematically reported. Previous studies provide summary descriptions of wider rodent populations including measures of species richness and diversity which are limited to providing evidence of potential contacts at a habitat level (Fichet‐Calvet et al. 2010; Bangura et al. 2021; Happi et al. 2022). The rich geolocation and temporal data provided by systematic rodent trapping can allow the estimation of direct or indirect rodent contacts through shared space utilisation over short timeperiods (Perkins et al. 2009; Clay et al. 2009). Inferred contact networks produced from these models of wildlife contact have previously been used to study pathogen transmission, particularly to investigate the importance of community structure or the effect of heterogeneities of contact rates between species in multi-host pathogen systems (Böhm, Hutchings, and White 2009; Drewe et al. 2011; White, Forester, and Craft 2017). Pathogens are more likely to persist in dense, well-connected networks where frequency dependent transmission dominates (Begon et al. 1999). In segmented or discontinuous networks, pathogens with limited environmental transmission will become locally extinct as the number of susceptible individuals is rapidly depleted (Swinton et al. 1998; Almberg et al. 2012).

Rodent communities are structured along anthropogenic land use gradients in the Lassa fever endemic region (**Chapter 3**; []). The prevalence of rodent hosts of LASV within human dominated land use types is expected to be higher in response to increased food availability, shelter availability and reduced predation pressure []. These factors also moderate rodent abundance and population dynamics which may promote increased pathogen persistence []. Understanding whether rodent contact networks vary along these anthropogenic land use gradients can elucidate the potentially different pathogen transmission networks in these settings. We therefore, hypothesise that rodent contact rates are greater in anthropogenically dominated habitats where nutritional resources are more concentrated.

Dominance of synanthropic, commensal, rodent species that are competent hosts of LASV within human dominated land use types might increase the density of rodent contact networks and reduce the betweenness of individual rodents within these communities []. Higher density networks with reduced betweenness are consistent with networks that support rapid pathogen transmission []. Therefore, if the majority of rodent contacts are within host competent intra-specific (i.e., between two members of the same species) contacts pathogen transmission will occur at greater rates []. We further hypothesise that spatial clustering of conspecifics and dominance of commensal species in these settings will lead to greater intra-specific contact rates compared to inter-specific contact rates. It is expected that rodent species’ with high contact rates will be associated with antibody positivity for LASV.

Here, we use rodent trapping data from a three-year study conducted in a Lassa fever endemic region, the Eastern Province of Sierra Leone, to reconstruct contact networks of rodent communities. We investigate the potential for direct and indirect contact among individual rodents in different land use settings. We reconstruct the contact networks of trapped individuals to investigate species and land use heterogeneity on the rate of contact within rodent networks with a particular focus on inter- and intra-specific contact rates of the primary host of LASV (*M. natalensis*). Finally, we report the prevalence of antibodies against LASV among rodents in our study region, exploring the association of contact rates with seropositivity.

# Methods

## Study area

Rodent trapping surveys were conducted between October 2020-April 2023 within and around four village study sites (Baiama; latitude = 7.8375, longitude = -11.2683, Lalehun; latitude = 8.1973, longitude = -11.0803, Lambayama; latitude = 7.8505, longitude = -11.1969, and Seilama; latitude = 8.1224, longitude = -11.1936) in the Lassa fever endemic zone of the Eastern Province of Sierra Leone. Surveys were conducted within trapping grids along a landuse gradient of anthropogenic disturbance comprising, forest, agriculture (including fallow and currently in-use areas), and villages (within and outside of permanent structures). Trapping survey sessions 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.

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 alongside acceptability of the study protocol to the village study site communities (see **Supplementary Text 1** for more details). Briefly, at each trapping grid 49 Sherman traps (7.62cm x 8.89cm x 22.86cm) (H.B. Sherman Traps, Tallahasee, USA), were placed in a 7 trap by 7 trap grid, traps were placed 10 metres apart in a grid conforming to the local landscape (median trapping grid area = 4,813m2). For traps placed within permanent structures trap placement deviated from the grid structure. Permanent structures were selected randomly 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. 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. Trapped rodents and shrews were associated with the coordinates of the trap they were detected in.

The sf package in the R statistical computing language (R version 4.1.2) was used for geospatial manipulation and analysis (Pebesma 2018; R Core Team 2021). All rodent handling was performed by trained researchers. Rodents and shrews were sedated with halothane and euthanised prior to obtaining morphological measurements and samples of blood and tissue following published guidance (Fichet-Calvet 2014). The study protocol was approved by the Clinical Research Ethical Review Board and Animal Welfare Ethical Review Board of the Royal Veterinary College, United Kingdom (URN: 2019 1949-3), and by the Research Ethics Committee of Njala University, Sierra Leone. Carcasses were incinerated after sample collection to eliminate the risk of onward pathogen transmission.

## Species identification

Species identification was performed in the field based on external characteristics using a taxonomic key, including external morphological measurements and characteristics, following Kingdon and Happold (Happold and Kingdon 2013) and Monadjem *et al.* (Monadjem et al. 2015) (**Supplementary Text 2**) Morphological identification alone is unable to distinguish some small-mammal species within the study area at species level. Therefore, molecular identification was performed on whole blood, tissue 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 (QIAGEN 2023) (Supplementary Text 2). DNA extracts were amplified using platinum *Taq* polymerase (Invitrogen) and cytochrome B primers (Bangura et al. 2021). DNA amplification was assessed through gel electrophoreisis with successful amplification products undergoing Sanger sequencing. Attribution of obtained sequences to rodent species was through the BLAST programme comparing NCBI species records for rodent cytochrome B to our sample sequences (Altschul et al. 1990) (**Supplementary Text 1**).

## Quantifying community contact networks

Species contact networks were reconstructed from the trapping data. Capture-mark-recapture (CMR) methods have previously been used to identify space-sharing by individuals (Carslake et al. 2005; Clay et al. 2009; Wanelik and Farine 2022). Within our study system a CMR design was not possible due to the risk of releasing an infected individual back into a human community. We therefore consider that rodents experience direct or indirect contacts with other individuals through detections at trapping locations co-located in time and space (Perkins et al. 2009). We assumed these potential contacts were sufficient to transmit LASV if they were trapped within a buffer zone of 30m radius (2,828 m2) from the location of the trap during the same 4 trap night session. A 30m radius was selected to encompass the potential home range of an individual. A strong assumption underlying this approach is that an individual was trapped at the center of their home range (Wanelik and Farine 2022). This buffer was applied to all species, further assuming that each species shared the same size home range.

We assessed the appropriateness of the choice of 30m as our buffer radius using the HomeRange R package (version 1.0.2) (Broekman et al. 2023). This software contains a dataset on the home ranges of 960 species, including 265 rodent and 17 shrew species. Four of these rodent species are included in our trapping data namely, *M. natalensis* our primary species of interest, *Lemnisomys striatus*, *Mus musculus* and *Rattus rattus*. For these species a 30m buffer is expected to contain the entirety of *M. natelensis* home ranges (mean home range = 419m2) and greater than 50% of the area of the home range of the remaining species (*L. striatus* = 83%, *M. musculus* = 92%, *R. rattus* = 52%) (**Supplementary Figure 1.**). To assess the importance of the assumption of buffer radius defining contacts and subsequent analyses we performed sensitivity analyses using buffer areas of 15m and 50m (**Supplementary Text 2**).

Networks were constructed from observed individuals (nodes) and the presence or absence of contacts between them (edges). Data were aggregated for land use type and sampling visit producing a potential 32 distinct networks from 201 trapping grid, village and visit combinations. However, as there were no detected rodents in three of the networks produced from forest sites, only 29 networks were used in subsequent analysis.

Within our trapping grids only a subset of all individuals are detected in traps. Including unobserved individuals, and therefore unobserved contacts between these individuals aids interpretation of network models, by providing a measure of the total population size that our analytic sample is derived from. Prior analysis of our study system suggests a probability of detection at each trap of less than 10% for 4 trap nights if the species is present in the trapping grid (**Chapter 3**). Therefore to estimate the abundance of individuals of each species within a trapping grid we modelled abundance (total population size) from repeated count data using an N-mixture model implemented in the unmarked R package (version 1.2.5) (Royle 2004; Fiske and Chandler 2011). The latent abundance distribution can be modelled as a Poisson, negative binomial or zero-inflated Poisson random variable. The abundance distribution was modelled with the number of trap nights and season as replicate dependent detection covariates in addition to location (whether a site was based in a rural or peri-urban setting) and landuse type (forest, agriculture or village) as occurrence covariates.

To select the most appropriate model for each species, the AIC of each of the Poisson, negative binomial or zero-inflated Poisson abundance distribution models were compared, with the best fitting model used to derive the estimated abundance. The median estimated abundance from the produced distribution at a trapping grid was then used to generate the unobserved individuals within each network aggregated to landuse type (**Supplementary Figure 2.1-2.12**). The number of observed individuals was then subtracted from the abundance to derive the number of unobserved individuals of each species. These unobserved individuals were explicitly set to have missing (i.e., unobserved) edge values.

Finally, the constructed adjacency matrices were converted to networks using the network R package (version 1.13.0.1) (Butts 2008). We describe these inferred contact networks stratified by land use and visit using network metrics including the number of nodes, the number of edges, median node degree, and network betweenness and density (**Supplementary Figure 3.1-3.29**). We further explore these contacts between individuals by reporting the characteristics of these observed contacts (i.e., inter- and intra-specific contacts) stratified by land use.

## Modelling the probablity of inter- and intra-specific contact rates in *Mastomys natalensis* across a land use gradient

To investigate whether land use and species are associated with the probability of a contact between two individuals we model these contacts as Exponential-Family Random Graphs (ERGM) (Hunter et al. 2008). Estimation of ERGM parameters provide an Odds Ratio (OR) for the probability of an edge in a network based on network properties included in the model and nodal attributes. ERGMs were specified for each of our inferred contact networks to compare the probabilities of edges forming based on rodent characteristics (i.e., species). The general model is shown in Equation 1:

Where is the number of terms in the model, the values of the coefficients represent the size and direction of the effects of the covariates on the overall probability of an edge being present in the network. At the edge level the expression for the probability of the entire graph can be re-expressed as the conditional log-odds of a single edge between two nodes (a contact between two rodents) as in Equation 2.

Here is the random variable for the state of the node pair and signifies all dyads in the network other than . is the coefficient for the change production of an edge between the two nodes conditional on all other dyads remaining the same ().

ERGMs are implemented using the ergm package (version 4.3.2) in R (Handcock et al. 2022). Three terms were included in the final ERGM to model the probability of the formation of ties (Equation 3.). The first term (edges), describes the density of the network and is the probability of a tie being observed in the network. The second term (species), is the conditional probability of a tie forming conditional on the species of the nodes. The third term (species homophily), is the conditional probability of a tie forming accounting for intraspecific tie formation among rodent individuals (i.e., the conditional probability of two individuals of the same species forming a tie). To reduce linear dependency of the nodal terms and due to data sparsity within our inferred networks all non-*M. natalensis* are grouped as “Other species” through the levels term of the nodal covariates for the analysis of the effect of land use on the probability of inter- or intra-specific contacts for *M. natalensis*.

ERGMs were implemented on the individual networks for each land use type at each visit. We pooled the effect sizes of each model through random-effects meta-analysis stratified by land use to produce a land use specific summary effect size for each coefficient []. Inclusion in meta-analysis was limited to ERGMs producing stable estimates for each of the model terms (i.e., sufficient detections of *M. natalensis* within the network). Random-effects models were conducted using the metafor package (version 4.0.0) in R (Viechtbauer 2010). The amount of heterogeneity was assessed using the restricted maximum-likelihood estimator with a prediction interval for the true outcomes produced [riley 2011]. Weights for each network in cluded in meta-analysis were assigned using inverse-variance weights []. The presence of influential networks was assessed using Cook’s distance, for models including influential networks leave-one-out sensitvity analysis were performed (Cheung 2019). Forest plots were produced to visualise the summary OR of the probability of a tie for each model term stratified by land use type [].

Models with unstable estimates for the species homophily term were not included in the random-effects meta-analysis. No contact networks from forest landuse contributed to meta-analysis as no *M. natalensis* were detected in these settings. Five models from agricultural settings and 6 from village settings were included in meta-analysis. Random effects models were specified using the metafor package (version 3.8-1) in R (Viechtbauer 2010). Effect sizes and standard errors for the three model terms were extracted. Weights for each network in the meta-analysis were assigned using inverse-variance weights. Two sensitivity analysis were performed first, by specifying a multi-level structure to the random-effects meta-analysis and second, by performing leave one-out meta-analysis (Cheung 2019).

## Quantifying *Lassa mammarenavirus* seroprevalence within small mammal communities

The BLACKBOX® LASV IgG ELISA Kit developed by the Diagnostics Development Laboratory hosted at the Bernhard Nocht Institute for Tropical Medicine and validated for rodent samples was used to determine serological status of trapped rodents (Gabriel et al. 2018; Soubrier et al. 2022). The full protocol is available as Supplementary Material 1. Briefly, 1 µL of whole blood was inactivated by mixing with the provided sample dilution buffer (1:50). Where whole blood was unavailable, blood was extracted from dried blood spots stored on filter paper by incubating with phosphate-buffered saline containing 0.08% Sodium Azide and 0.05% Tween-20 [gruner]. Samples alongside negative and positive controls were incubated on the provided ELISA plates for 24 hours at 4-8 °C in a wet chamber. Following incubation, the plates were washed and incubated for a further hour with 1:10,000 diluted HRP-labelled streptavidin. A final wash was performed prior to the addition of 100µL of 3,3’,5,5’-Tetramethylbenzidine (TMB) substrate to wells, with incubation for 10 min. The colorimetric reaction was stopped by adding 100µL of a stop solution.

In a deviation from the kit protocol the optical density (OD) at 450nm and 630nm was measured (as opposed to 450nm and 620nm). The index value was produced from the OD difference (OD450-OD630) divided by the cut-off values (the mean values of the negative controls + 0.150). Samples were considered positive with index values greater or equal to 1.1, negative results less than or equal to 0.9, and inconclusive results when the index value lay between 0.9 and 1.1. Inconclusive results were repeated as advised by the kit manufacturers.

We investigated whether small mammal species with individuals seropositive for LASV were more likely to have an increased number of observed contacts (i.e., increased degree) or if these positive individuals were members of more densely connected networks (i.e., increased betweenness).

# Results

Overall 684 small mammals were trapped from 43,266 trap-nights. Seventeen species were identified, 13 of which were rodent species (76%) with four species of insectivorous shrews identified (24%). *Mastomys natalensis* was the most commonly detected species (N = 113, 16.5%), followed by *Crocidura olivieri* (N = 105, 15.3%) and *Praomys rostratus* (N = 102, 15%) (Table 1.).

## Small mammal community contact networks

**Needs updating** Rodent contact rates, while heterogeneous, are similar across landuse types. Networks produced from rodents trapped in agricultural landuse settings contained the highest species richness (median = 10, IQR = 1), followed by village (median = 8, IQR = 1) and forest (median = 6, IQR = 0.5). More individuals (nodes) were observed and predicted in agricultural landuse (median = 988, IQR = 118) than village (median = 447, IQR = 317) and forest (median = 163, IQR = 32.5) (Figure 1A.). The number of observed contacts (edges) followed a similar pattern with a greater number of edges observed in agricultural settings (median = 38, IQR = 47) followed by village (median = 26, IQR = 19) and forest landuse (median = 3, IQR = 16.5) (Figure 1B.). Network density, was similar in village and agricultural settings (median = 0.06 and 0.09 respectively) but higher in forest settings (median = 0.44) where fewer individuals were observed.

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The median degree (number of edges) of a node were similar across all landuse types (Figure 2A.). Within forest landuse types no rodents had a degree greater than 6, the highest degree was 19 and 17 in agricultural and village landuse respectively. The median number of contacts did not importantly differ by species (Figure 2B.). Within species there was substantial variability in degree between individual rodents, for example, the median degree of *Praomys rostratus* in agricultural landuse was 3, although 3 individuals had a degree of greater than 15.

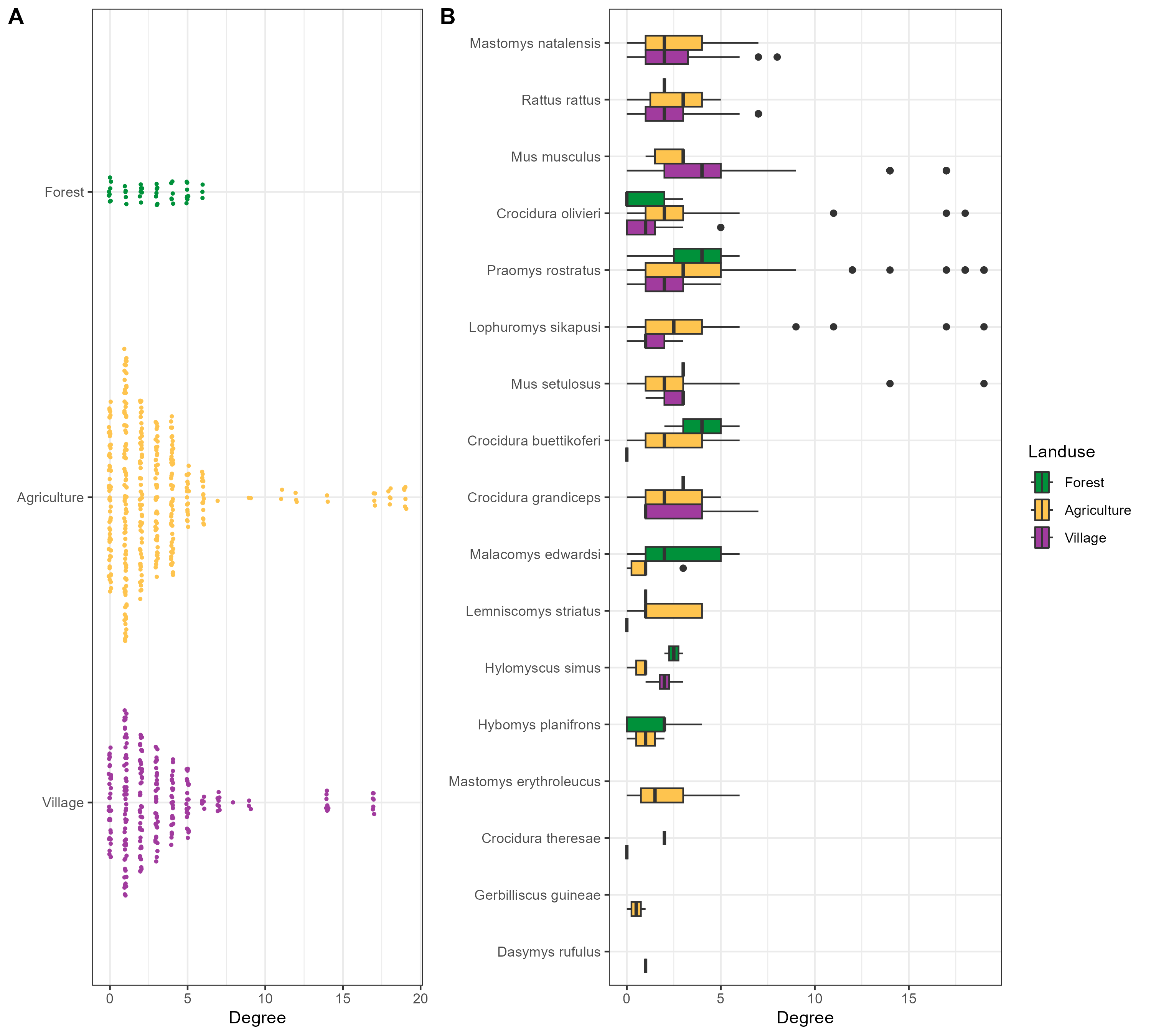
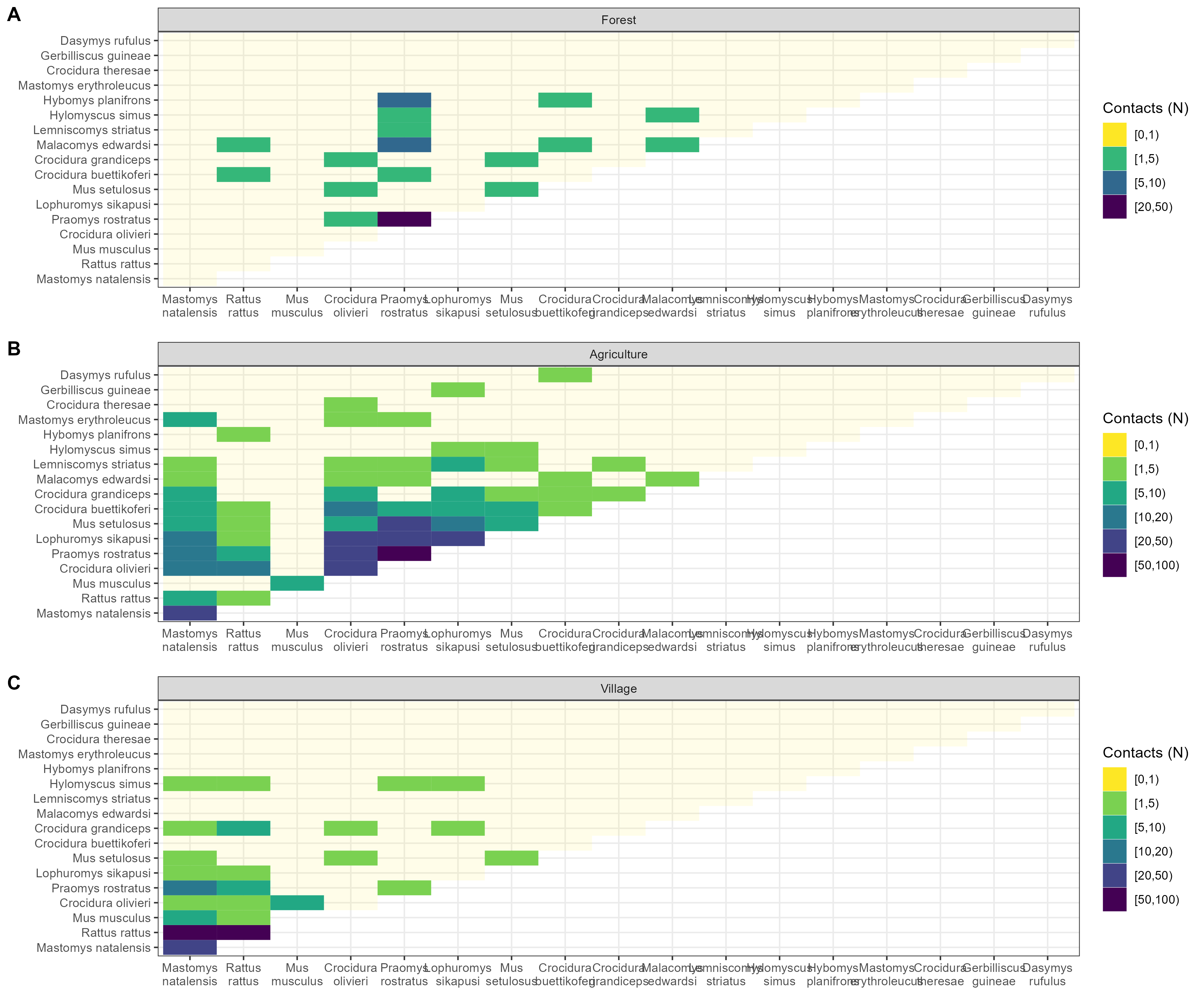


Figure 2: A) The degree of each observed rodent within the produced networks grouped by landuse type. B) The distribution of degree within the networks grouped by the species of the observed individual and the landuse type in which they were detected.

## Describing contacts within and between species in rodent communities

Species had high variability in the number of other species they had contact with, for example *M. natalensis*, *P. rostratus* and *R. rattus* had contacts with 9 other rodent species while *M. musculus* had 3 (Figure 3.). There was a general trend that the species with more individuals observed had greater number of contacts with other species (*r(11)* = 0.78, *p* < 0.005). *M. musculus* is an important outlier to this trend, it was the fourth most observed species but had few observed contacts with other species. Intraspecific contacts dominated the edges between individual rodents of most species, across all landuse types, particularly among the most commonly observed species. *Mastomys natalensis* was found to have contacts with 8 other species in agricultural landuse and 5 in village landuse settings, in agricultural settings most contacts were observed to be intra-specific while in villages interspecific contacts with *R. rattus* were more commonly observed than both intra-specific contacts and contacts with another commensal species, *P. rostratus*.

**Change to rate of contacts, to-from and from-to species or the proportion of all contacts of that species that are between those species** 

All six species containing individuals found to be LASV antibody positive in this study were found to have contact with *M. natalensis*, the primary reservoir of LASV, either in agricultural or village landuse settings.

## The probability of inter- and intraspecific contact rates of *Mastomys natalensis* across a land use gradient

Limiting our analysis of the probability of a contact being observed to the primary reservoir species of LASV, *M. natalensis*, resulted in 12 of the constructed networks being suitable for random effects meta-analysis. Five agricultural and 6 village land use networks were included in meta-analysis (Figure 3.). The odds of a contact being observed in these networks were generally low with similar odds across both agricultural (Odds Ratio = 0.08, 95% Confidence Interval = 0.04-0.13, *p* < 0.001) and village land use (OR = 0.1, 95% C.I. = 0.06-0.16, *p* < 0.001) (Figure 4A.). There were high levels of heterogeneity in the odds of a contact being observed between networks from different visits for both agricultural and village settings ($\hat{\tau}^2\_{\text(agriculture)}$ = 0.38, = 98, *p* < 0.001 and $\hat{\tau}^2\_{\text(village)}$ = 0.19, = 27.2, *p* < 0.001). The low probability of an edge being observed across all visits and land use types is consistent with contacts within these communities are sparse.

*Mastomys natalensis* had a statistically significantly reduced odds of forming a contact with a different small mammal species (i.e., an inter-specific contact) in agricultural (OR = 0.48, 95% C.I. = 0.24-0.97, *p* = 0.04) and village settings (OR = 0.61, 95% C.I. = 0.39-0.99, *p* = 0.046) when compared to inter-specific contacts among other species in these communities (the reference). There were high levels of heterogeneity in the odds of inter-specific contacts being observed between networks ($\hat{\tau}^2\_{\text(agriculture)}$ = 0.45, = 19.5, *p* < 0.001 and $\hat{\tau}^2\_{\text(village)}$ = 0.19, = 13.4, *p* = 0.04). *Mastomys natalensis* was less likely to come into contact with individuals of a different species than other species within our communities.

Finally, *M. natalensis* had a statistically significant increased odds of forming contacts with other individuals of the same species (i.e., an intra-specific contact) in agricultural (OR = 5.58, 95% C.I. = 2.67-11.7, *p* < 0.001) but not in village settings (OR = 2.24, 95% C.I. = 0.89-5.64, *p* = 0.08) when compared to inter-specific contacts among non-*M. natalensis* species. There was no substantial heterogeneity in the analysis of the odds of intra-specific contacts ($\hat{\tau}^2\_{\text(agriculture)}$ = 0, = 1.7, *p* = 0.78 and $\hat{\tau}^2\_{\text(village)}$ = 0.45, = 7.48, *p* = 0.27) in both land use types. *Mastomys natalensis* compared to other small mammal species was more likely to have intra-specific contacts within communities in agricultural but not village settings.

In the first sensitivity analysis altering the radius in which a contact was defined there was no change in direction of the effect sizes for the random-effects meta-analysis (**Supplementary Text 3**). There were no important changes in effect size direction or magnitude in leave-one-out sensitivity testing for meta-analyses including influential networks. The results of these sensitivity analyses suggest that our results are robust to the assumption of contact range and any changes to the rodent community over time.

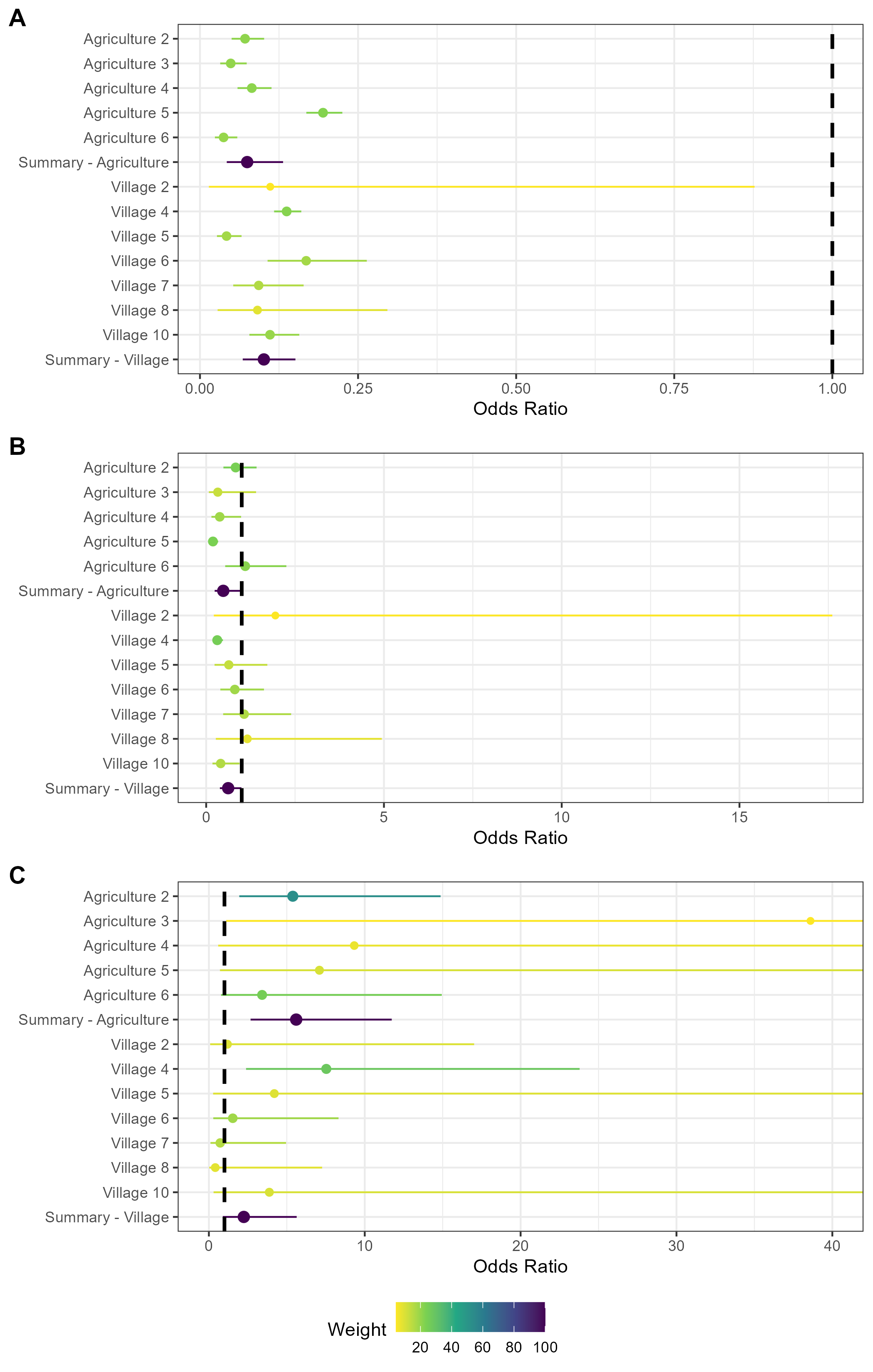


Figure 4: Random effects meta-analysis of ERGM network models investigating the odds of a contact being observed for *M natalensis*. A) The odds ratio of a contact being observed for *M. natalensis* in Agricultural or Village landuse types. B) The odds ratio of a contact being observed between *M. natalensis* and an individual of a different rodent species. C) The odds ratio of a contact being observed between *M. natalensis* and another *M. natalensis*.

## Prevalence of *Lassa mammarenavirus* antibodies within small mammal communities

601 individual rodents were trapped from 37,982 trap-nights (TN). 13 species were identified from molecular classification, the majority of which were identified as *M. natalensis* (N = 102, 17%), *Praomys rostratus* (N = 88, 14.6%) and *Mus musculus* (N = 73, 12.1%) (Table 1.). Antibodies to LASV were identified in 20 rodents (20/601, 3.3%) from 6 species, including *M. natalensis* (7/20, 35%), 5 *Crocidura spp.* (5/20, 25%), 3 *L. sikapusi* (3/20, 15%) and 3 *Mus setulosus* (3/20, 15%) (Table 1.). The highest proportion of positivity was observed in *Malacomys edwardsi* (1/11, 9%), *Mus setulosus* (3/38, 7.9%) and *M. natalensis* (7/102, 6.8%).

| Species | Indviduals (N) | LASV Antibody detected (%) | Percentage of all positive individuals |
| --- | --- | --- | --- |
| *Mastomys natalensis* | 113 | 6 (5.3%) | 30% |
| *Crocidura olivieri* | 105 | 5 (4.8%) | 25% |
| *Lophuromys sikapusi* | 57 | 3 (5.3%) | 15% |
| *Mus setulosus* | 43 | 3 (7%) | 15% |
| *Rattus rattus* | 88 | 1 (1.1%) | 5% |
| *Malacomys edwardsi* | 11 | 1 (9.1%) | 5% |
| *Mastomys erythroleucus* | 4 | 1 (25%) | 5% |
| *Praomys rostratus* | 102 | 0 (0%) | 0% |
| *Mus musculus* | 90 | 0 (0%) | 0% |
| *Crocidura buettikoferi* | 23 | 0 (0%) | 0% |
| *Crocidura grandiceps* | 15 | 0 (0%) | 0% |
| *Lemniscomys striatus* | 11 | 0 (0%) | 0% |
| *Hylomyscus simus* | 9 | 0 (0%) | 0% |
| *Hybomys planifrons* | 7 | 0 (0%) | 0% |
| *Crocidura theresae* | 3 | 0 (0%) | 0% |
| *Gerbilliscus guineae* | 2 | 0 (0%) | 0% |
| *Dasymys rufulus* | 1 | 0 (0%) | 0% |

Rodents with antibodies to LASV were detected in three of the study villages, Lalehun (N = 11, 55%), Seilama (N = 8, 40%) and Baiama (N = 1, 5%). Lalehun had the highest percentage of antibody positive rodents (11/146, 7.5%), followed by Seilama (8/247, 3.2%) and Baiama (1/96, 1%), no positive rodents were detected in the most urbanised village Lambayama. Antibody positive rodents were detected in all landuse types, most positive rodents were trapped in agricultural landuse (13/20, 65%), followed by village (6/20, 30%) and forest (1/20, 5%) settings. The proportion of antibody positive individuals among all rodents trapped were similar across forest (1/40, 2.5%), agricultural (13/339, 3.8%) and village (6/222, 2.7%) landuse types. Antibody positive rodents were detected during all sampling visits, the proportion of rodents testing positive were similar between the dry (11/364, 3%) and rainy (9/237, 3.8%) seasons.

We did not observe any important difference in the median number of contacts for species that were found to be LASV antibody positive.

# Discussion

In our study within the Eastern province of Sierra Leone, we found that small mammal community contact networks while generally larger had similar rates of contact across a land use gradient from forest, through agriculture to village settings. We found that most individuals had fewer than 5 contacts, with few individuals from a limited number of species having more than 10 contacts. There was no clear difference in degree by species across different land use types. For *M. natalensis* specifically, we found that they were less likely to form inter-specific contacts than intra-specific contacts and that despite a similar number of contacts within both agriculture and village settings there was some evidence for a higher probability of these intra-specific in agricultural settings. Finally, we found low prevalence of seropositivity to LASV within these small mammal communities in four villages in the Eastern province of Sierra Leone. Antibodies to LASV were detected in 6 rodent and shrew species with the majority of seropositive individuals belonging to *M. natalensis* trapped from X settings. This is potentially important for the dynamics of LASV transmission in these settings and suggests that pathogen transmission within the rodent community may occur at greater rates in agricultural rather than village land use.

As hypothesised our analysis suggests that while agricultural settings and villages contained more contacts than forests ….. We hypothesised that intra-specific contact rates would be greater than inter-specific contact rates. For *M. natalensis* our analysis supported this hypothesis in agricultural settings where the odds of intra-specific contacts were significantly greater than inter-specific contacts despite these settings having high species richness. This was not supported in village landuse settings were intra-specific contacts were not significantly greater than inter-specific contacts.

The number and proportion of seropositive rodents detected in the current study, while low (3.3%), was similar (2.8%) to that reported by another study that sampled rodent populations in Eastern Sierra Leone (Bangura et al. 2021). Comparison of these studies is limited by different sampling design as we sampled rodents in forest environments and locations more distant from areas of human habitation. The proportion of all seropositive individuals that were *M. natalensis* (30%) was lower in our study than in the study conducted in the neighbouring district (75%) although the proportion of all *M. natalensis* that were antibody positive was more similar (5.3% compared to 8%). We similarly identified antibodies in *L. sikapusi* and *R. rattus*. Antibodies to LASV were identified in three further species, *Crocidura olivieri*, *Mus setulosus* and *Mastomys erythroleucus* that were not reported from the Bangura study. Antibodies to LASV have not previously been reported in *M. setulosus*. We did not detect antibodies in any samples from *Praomys rostratus*. Our results support previous studies’ findings that evidence of prior acute infection is present in multiple species within rodent communities in West Africa (Demby et al. 2001; Agbonlahor et al. 2017; Bangura et al. 2021).

We found that while contact networks within forest settings had higher densities, these networks contained fewer individual rodents and fewer species than agricultural settings where the total number of individuals, the total number of contacts and the number of contacts each individual made was greatest. Village landuse settings shared more similarities with agricultural landuse, although with fewer species detected. The number of species containing individuals that made the greatest number of contacts was occurred in agricultural settings with four species having individuals with more than 10 contacts, compared to village settings where only a single species (*M. musculus*) had individuals with more than 10 contacts. None of the individuals of *M. natalensis* were identified to have more than 8 contacts.

*Mastomys natalensis* was found to have significantly fewer contacts than the other rodent species within the rodent communities in agricultural settings but not in village settings. When contacts were observed for this species in agricultural settings they were statistically significantly higher odds of these being intra-specific contacts compared to contacts with other species. This was not replicated in village settings suggesting that space sharing with other species was more common in village settings. This is in agreement with prior research suggesting that this species does not exhibit strong territorial responses, similar to *R. rattus* but not *M. musculus* (Borremans et al. 2014; Whisson, Quinn, and Collins 2007; Anderson 1961). Homophily in contacts of *M. natalensis* may be important for viral transmission if other species are not as effective hosts for LASV replication and transmission. For example, if an infected individual resides in an agricultural setting it has higher odds of having a contact sufficient to transmit LASV during its infectious period compared to if that individual was located in village settings. This may result in different pathogen dynamics by landuse type. In agricultural settings a greater force of infection may exist where following viral introduction susceptible individuals are infected during a shorter period but, population level immunity is rapidly reached, leading to local pathogen extinction. The same may not be the case in village settings where an infected rodent may have fewer contacts and thus LASV transmits at a slower rate but is able to persist due to rapid replenishment of susceptible individuals. This may be complicated further by migration of individuals between agricultural and village settings based on resource availability as has been reported in this species from studies conducted in Guinea (Mari Saez et al. 2018). The changing risk to human populations from outbreaks of Lassa fever is thus likely governed by contact among susceptible rodents in the local environment which may be dynamic.

We did not detect a sufficient number of seropositive individuals to directly model the potential transmission networks of LASV through rodent communities in these different landuse settings. Ideally transmission networks should be developed from acute infection data rather than seroprevalence. Based on prior results suggesting that fewer individuals will be PCR positive than seropositive, it is unlikely that sufficient data would be available to parameterise models of transmission networks without increasing the number of sampling periods and locations. Future studies in the Eastern province of Sierra Leone will benefit from recent studies, including this one, when estimating the population level seroprevalence to calculate the required trapping effort to obtain sample sizes required to parameterise transmission models.

Several important assumptions were made that should be considered when contextualising the results of this research. First, we were unable to explicitly observe direct and indirect contacts among rodents in our study. To infer these contacts we utilised co-location of trapped individuals in time and space. This assumed that individuals were detected at the centroid of their home range and that they spend an equivalent amount of time at all points within the area of their home range. It is unlikely that this assumption holds true in our study system and this will lead to different contact rates than we infer in our networks (Wanelik and Farine 2022). Modifications to the current study design to explore the impact of these assumptions could include radio tagging or fluorescent marking to monitor rodent contacts in real-time. Second, only a small proportion of rodents active within a study site would be detected by our trapping activity. We account somewhat for this by inferring the total abundance of species within these sites. However, if individuals that were detected display importantly different behaviours than those not detected then inferring across these populations may be problematic. For example, if trap shyness is associated with inter- or intra-specific space sharing then detection of less trap shy individuals may overestimate the number of contacts individuals of a species are likely to make.

In conclusion this study has highlighted the variability of inter- and intra-specific contact rates between different rodent species in different land use types in a setting of rodent borne zoonotic disease risk. We propose that the wider rodent community produces more complex transmission networks for LASV than previously assumed, this is supported by the number of different rodent species that have been found to be infected with LASV both within this study and in the prior literature.

# Supplementary material

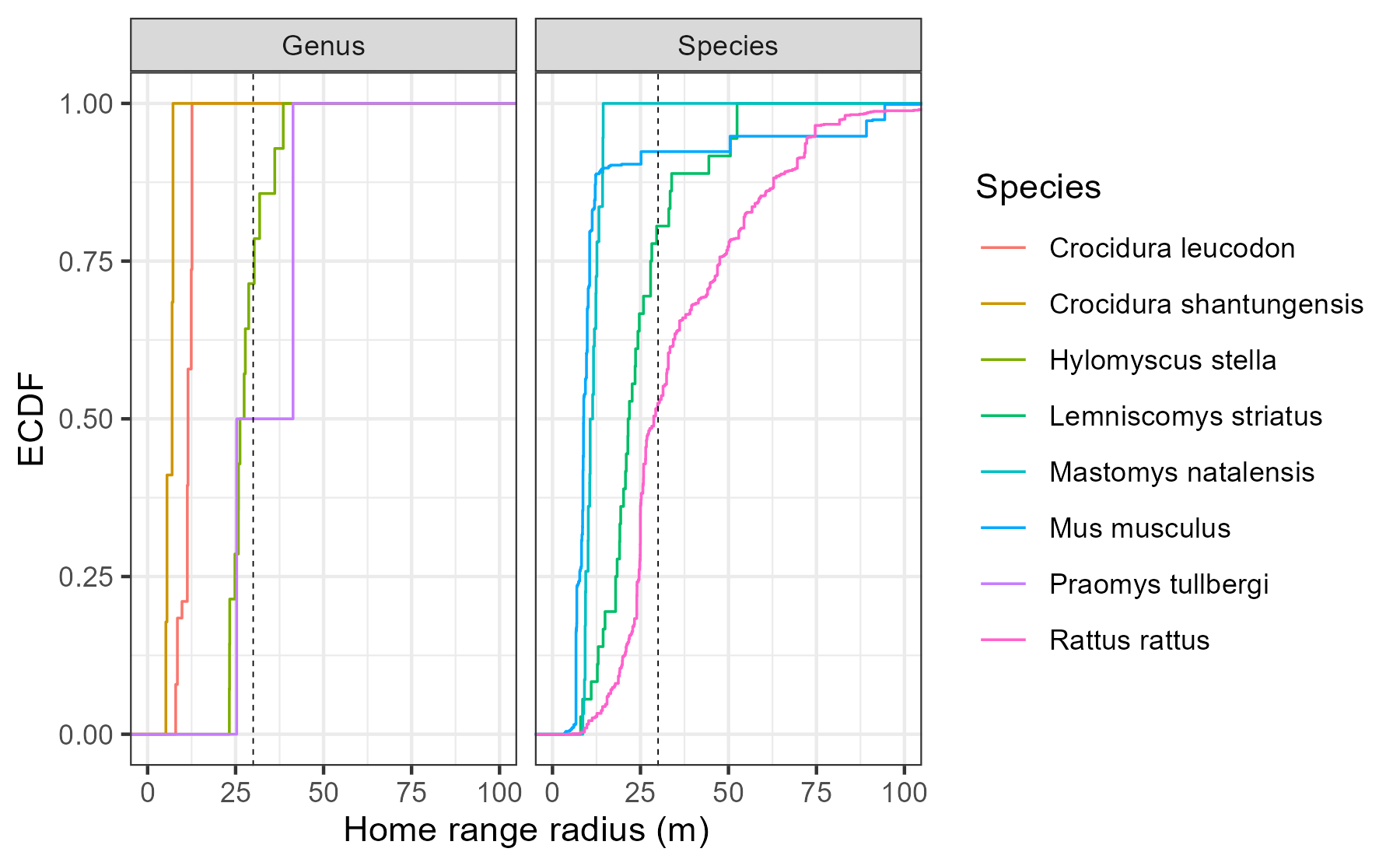
## Supplementary Material 1

Attached to the email, contains the protocols for the trapping and lab work.

## Supplementary Material 2

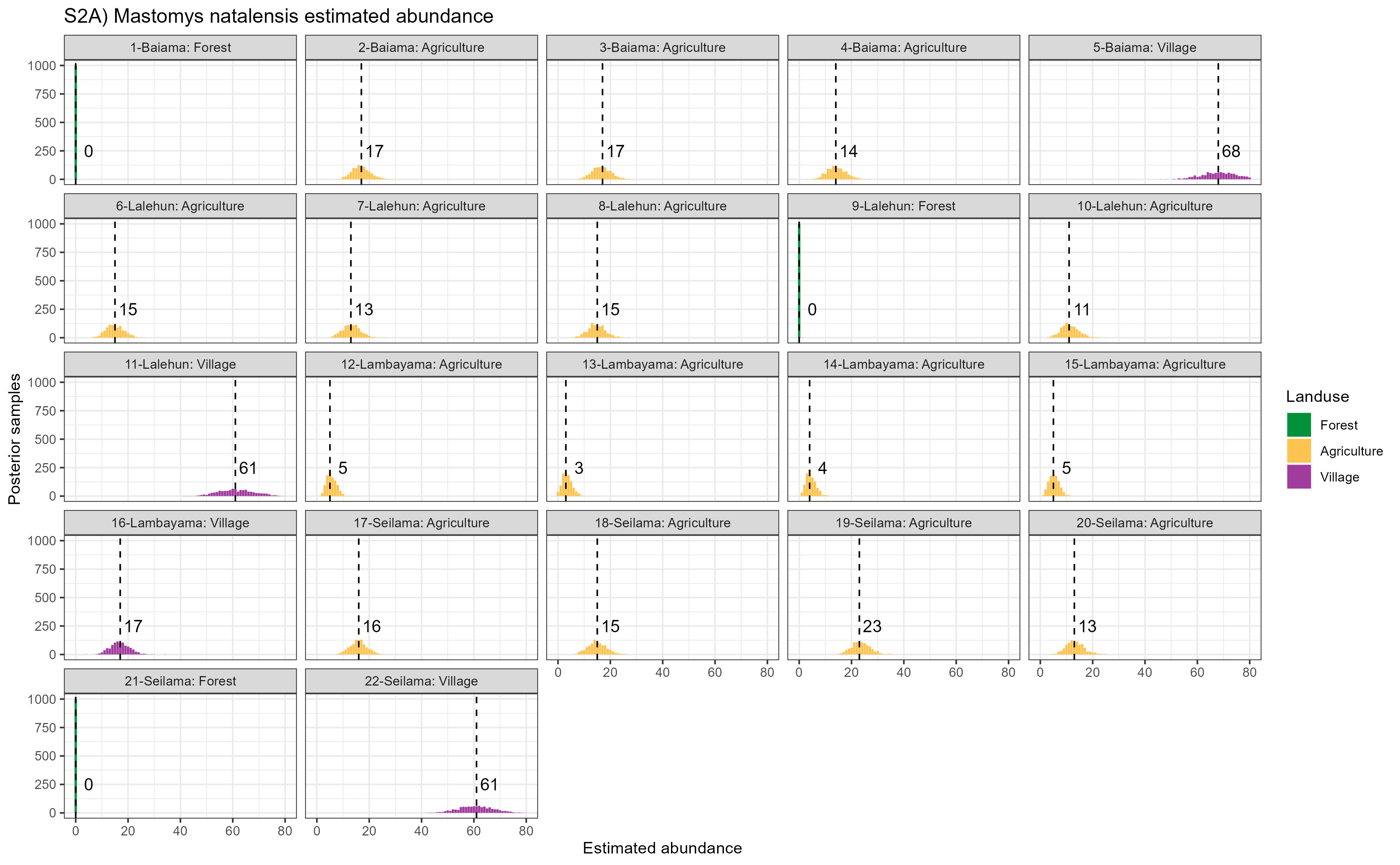
Attached to the email, contains the morphological taxonomic key.

## Supplementary Figure 1

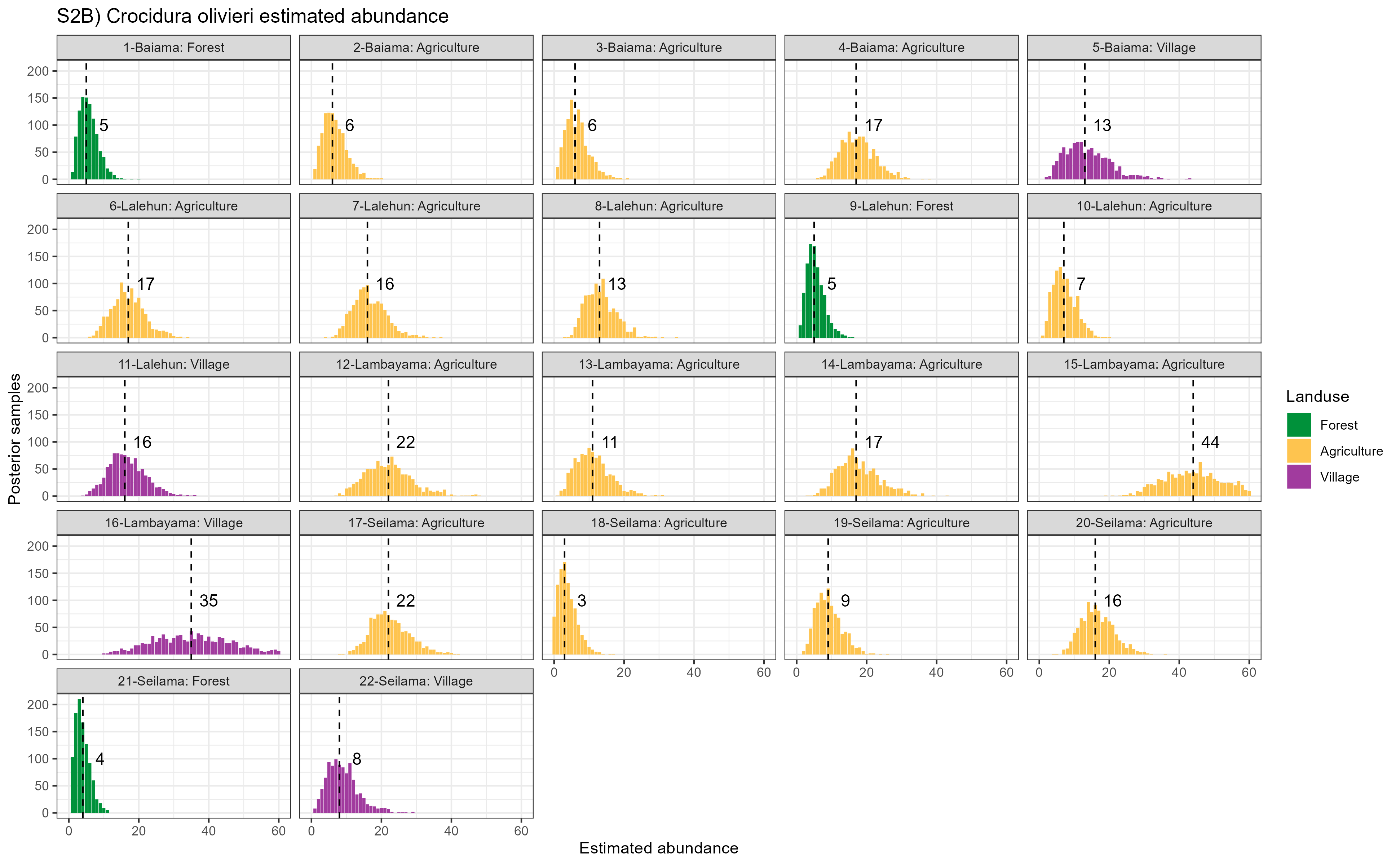


Supplementary Figure 1: Empirical Cumulative Density Function of the home range radius of rodent and shrew species with data available in the HomeRange dataset. Species that match detected genera in our study include two shrew species *Crocidura leucodon* and *Crocidura shantungensis* and two rodent species *Hylomyscus stella* and *Praomys tullbergi*. Four species matches to rodent species detected in our study were also included *Lemniscomys striatus*, *Mastomys natalensis*, *Mus musculus* and *Rattus rattus*. Only *Lemniscomys striatus* and *Mastomys natalensis* contain data from Africa (Uganda and Tanzania respectively). The dashed line represents the 30m range radius used for the primary analysis in the current study.

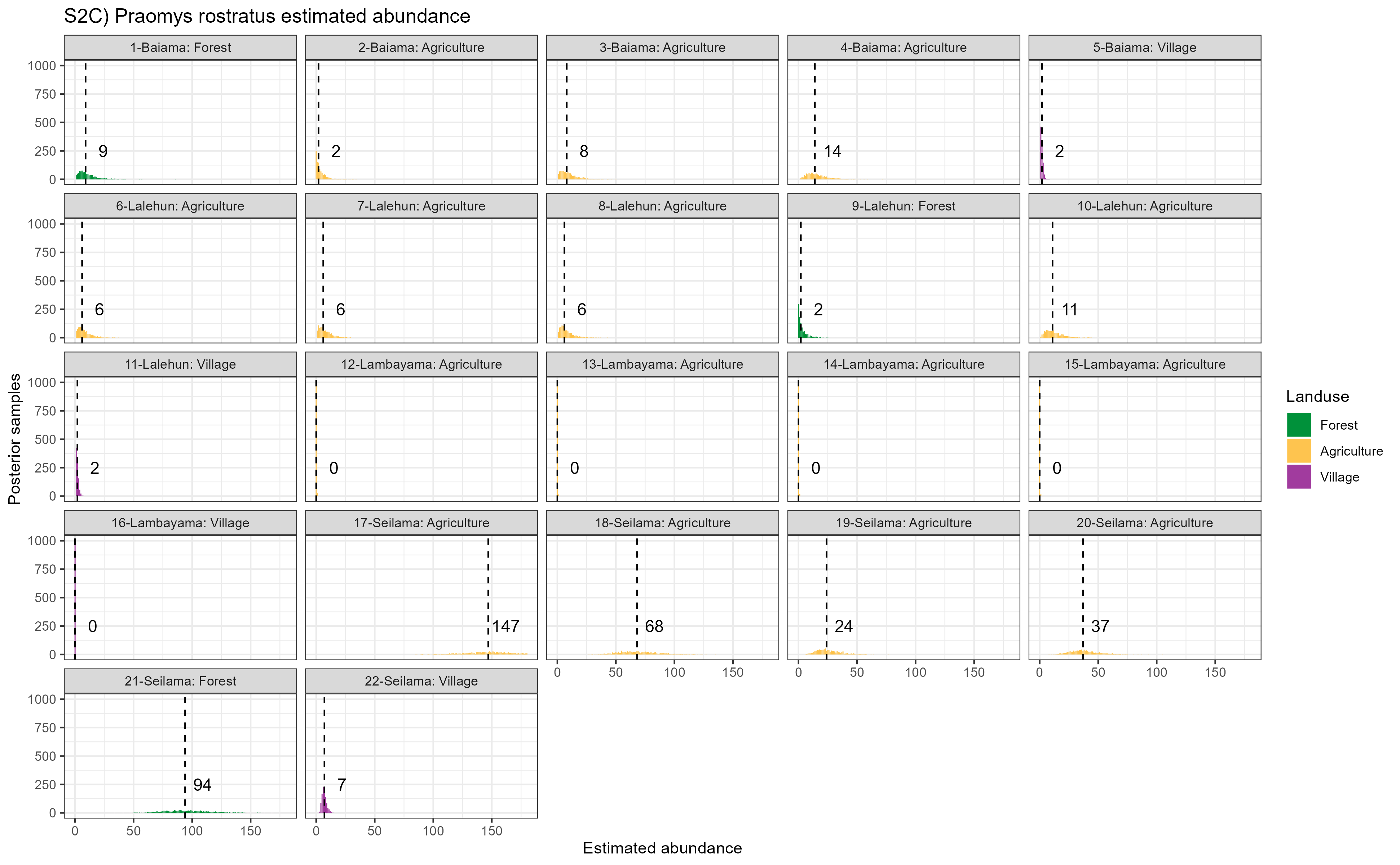
## Supplementary Figure 2A-F



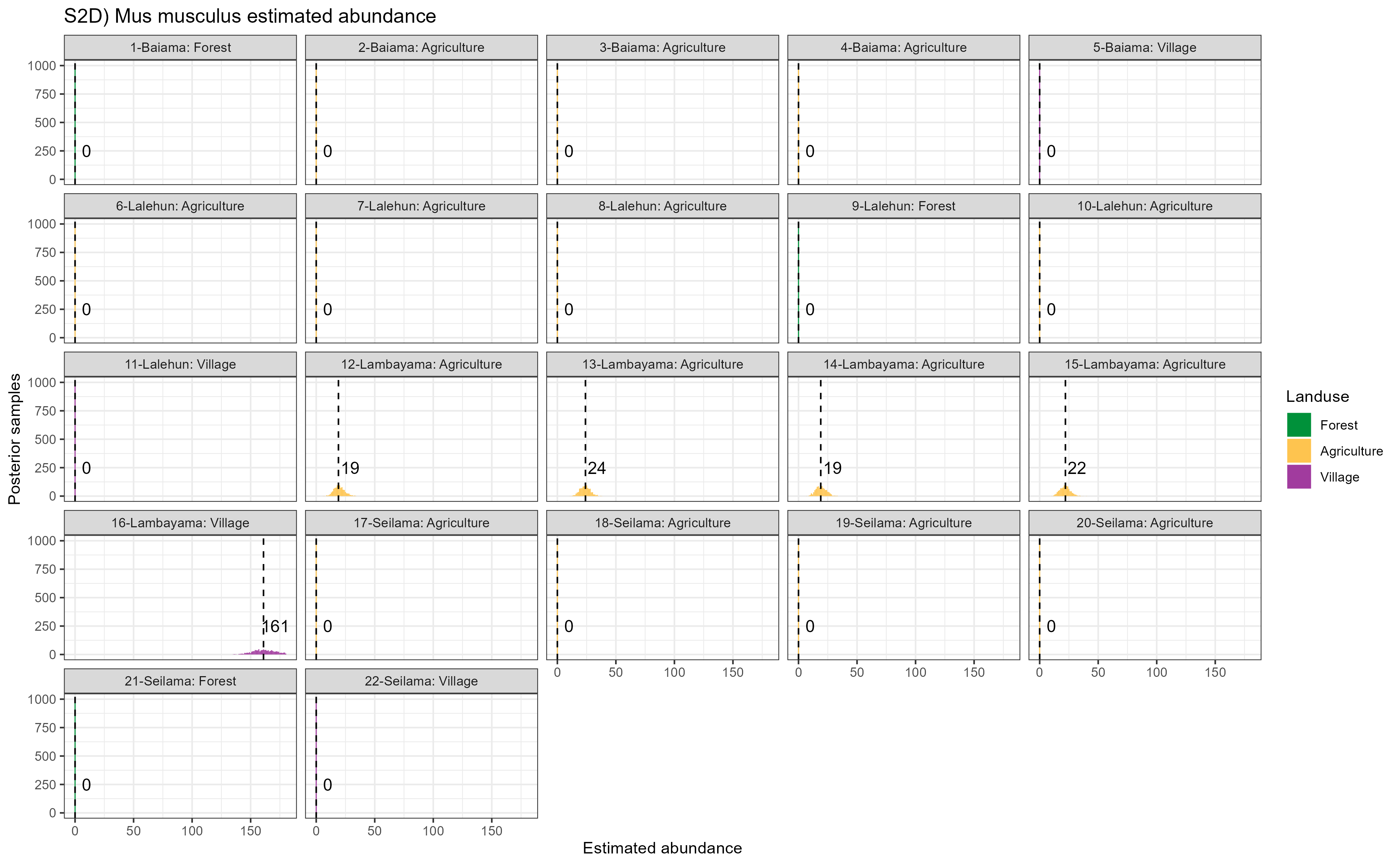
Supplementary Figure 2A: Estimated abundance at each sampling site for *Mastomys natalensis*. The dashed line and number is the median abundance used to infer the population size at this study site.



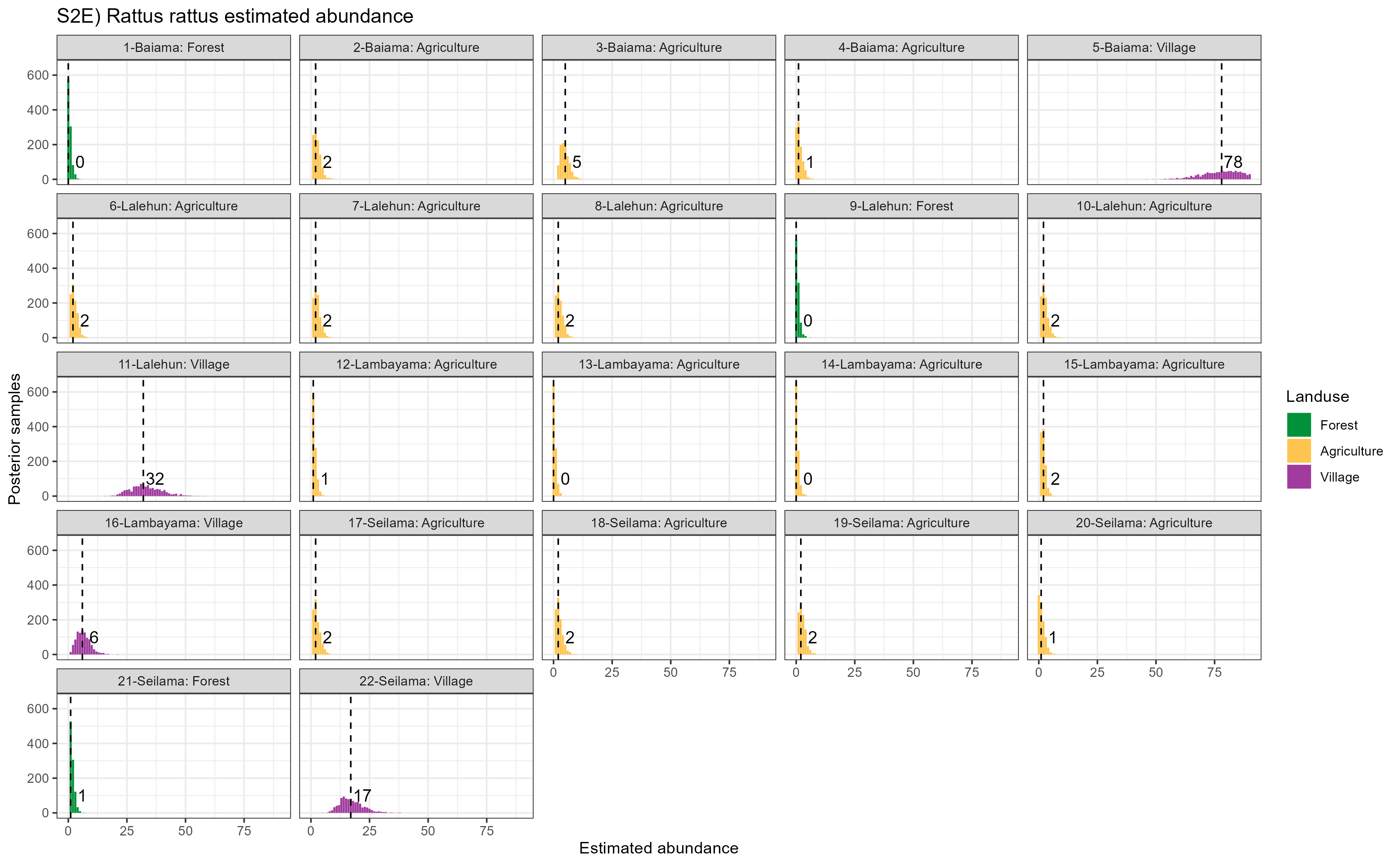
Supplementary Figure 2B: Estimated abundance at each sampling site for *Mus musculus*. The dashed line and number is the median abundance used to infer the population size at this study site.



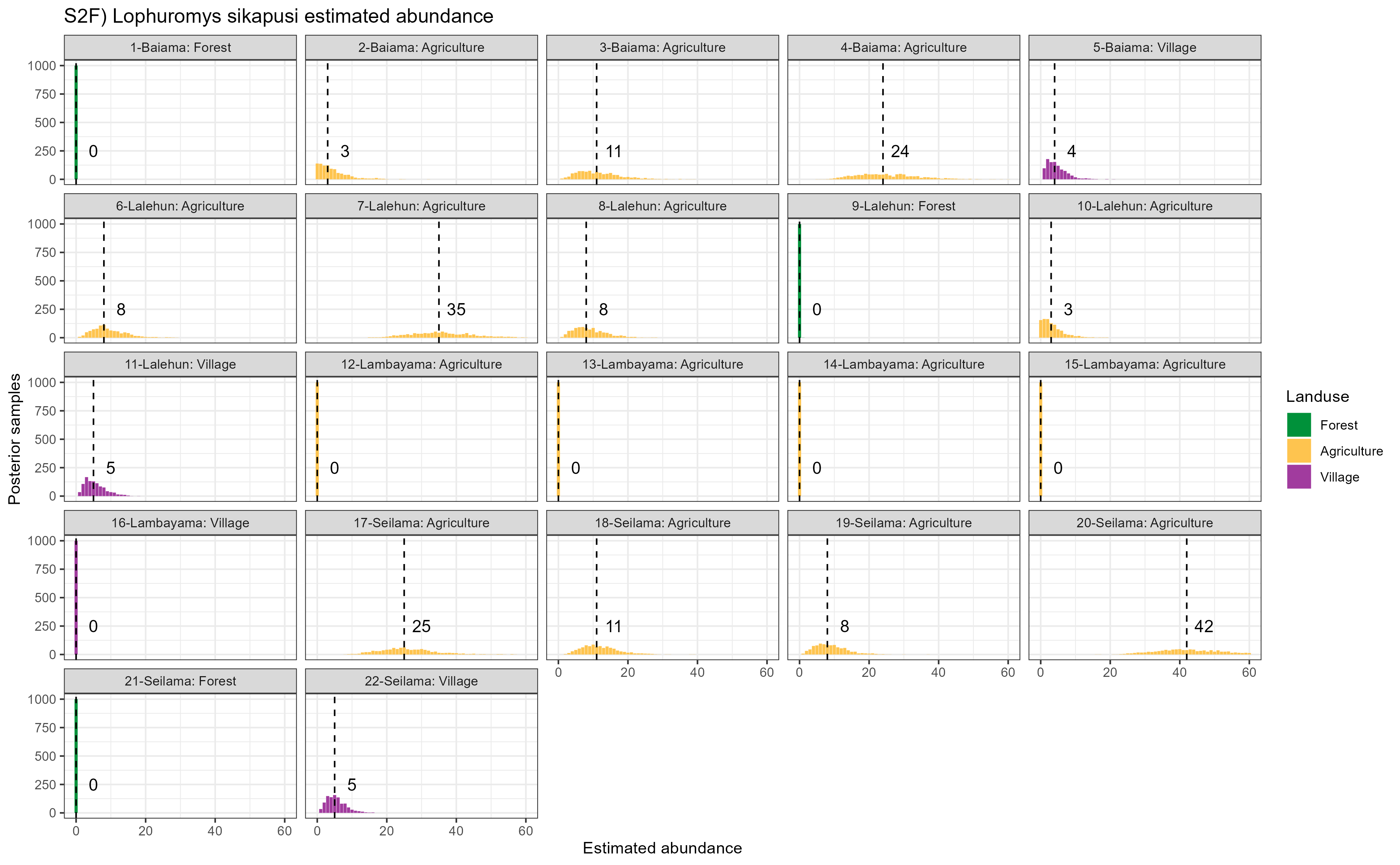
Supplementary Figure 2C: Estimated abundance at each sampling site for *Rattus rattus*. The dashed line and number is the median abundance used to infer the population size at this study site.



Supplementary Figure 2D: Estimated abundance at each sampling site for *Crocidura spp*. The dashed line and number is the median abundance used to infer the population size at this study site.



Supplementary Figure 2E: Estimated abundance at each sampling site for *Praomys spp*. The dashed line and number is the median abundance used to infer the population size at this study site.



Supplementary Figure 2F: Estimated abundance at each sampling site for all other species (species with fewer than 20 observations). The dashed line and number is the median abundance used to infer the population size at this study site.

## Supplementary Figure 3A-W

These are the networks produced for each landuse type and visit. I have not included them in this file but they are attached to the email in a .zip file if of interest.

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