

1 **Local human movement patterns and land use impact exposure to zoonotic malaria in Malaysian**

2 **Borneo**

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26

27 **Abstract: (150 max)**

28

29 Human movement into insect vector and wildlife reservoir habitats determines zoonotic disease
30 risks; however, few data are available to quantify the impact of land use on pathogen transmission.
31 Here, we utilise GPS tracking devices and novel applications of ecological methods to develop fine-
32 scale models of human space use relative to land cover to assess exposure to the zoonotic malaria
33 *Plasmodium knowlesi* in Malaysian Borneo. Combining data with spatially explicit models of
34 mosquito biting rates, we demonstrate the role of individual heterogeneities in local space use in
35 disease exposure. At a community level, our data indicate that areas close to both secondary forest
36 and houses have the highest probability of human *P. knowlesi* exposure, providing quantitative
37 evidence for the importance of ecotones. Despite higher biting rates in forests, incorporating human
38 movement space use into exposure estimates illustrates the importance of intensified interactions
39 between pathogens, insect vectors and people around habitat edges.

40

41

42 **Keywords (min 3):**

43 Disease ecology, spatial epidemiology, *Plasmodium knowlesi*, malaria, human movement, land use

44

45 **Introduction:**

46

47 Environmental change and human encroachment into wildlife habitats are key drivers in the
48 emergence and transmission of zoonotic diseases (1, 2). Individual movements into different
49 habitats influence exposure to disease vectors and animal reservoirs, determining risk and
50 propagation of vector-borne diseases (3-5). Increased contact between these populations is
51 theorised to drive increases of the zoonotic malaria *Plasmodium knowlesi* in Malaysian Borneo, now
52 the main cause of human malaria within this region. *P. knowlesi* is carried by long- and pig-tailed
53 macaques (*Macaca fascicularis* and *M. nemestrina*) and transmitted by the *Anopheles leucospyphus*
54 mosquito group, both populations highly sensitive to land cover and land use change (6). Although
55 higher spatial overlap between people, macaques and mosquito vectors likely drives transmission,
56 the impact of human movement and land use in determining individual infection risks is poorly
57 understood (7).

58

59 The emergence of the zoonotic malaria *Plasmodium knowlesi* has been positively associated with
60 both forest cover and historical deforestation (8, 9). However, out of necessity, statistical
61 approaches to assess environmental risk factors for *P. knowlesi* and other infectious diseases
62 typically evaluate relationships between disease metrics and local land cover surrounding houses or
63 villages. While an individual may spend most of their time within the vicinity of their residence, this
64 area does not necessarily represent where they are most likely to be exposed to a disease. This is
65 supported by varying associations between *P. knowlesi* occurrence and landscape variables at
66 different distances from households, ranging from 100m to 5km, likely partially due to human
67 movement into different surrounding habitats (8, 10). Although land cover variables describing
68 physical terrestrial surfaces are frequently incorporated into disease models, land use is rarely
69 quantified. Land use is commonly defined as “the arrangements, activities, and inputs that people
70 undertake in certain land cover types” (11). Places with similar types of land cover may be used very

71 differently, with the activities and frequencies with which people visit these places determining the
72 spatial distribution of disease (1).

73

74 Mathematical modelling studies have revealed the importance of spatial variation in contact rates
75 due to the movement of individuals through heterogeneous environments with varying transmission
76 intensity (12). A multi-species transmission model of *P. knowlesi* highlighted the role of mixing
77 patterns between populations in different ecological settings in determining the basic reproductive
78 rate and subsequent modelling studies illustrate the sensitivity of this disease system to population
79 densities of both people and wildlife hosts (7, 13). However, although mechanistic models have been
80 extended to explore the potential importance of these heterogeneities in disease dynamics, there
81 are inherent constraints on model complexity and most models make simplistic assumptions about
82 the habitat uses of different populations.

83

84 Empirical data on human population movement is increasingly available, allowing assessment of the
85 impact of mobility on infectious disease dispersion and risks (5). On larger spatial scales, mobile
86 phone data has revealed the role of human migration in the transmission of infectious diseases such
87 as malaria, dengue and rubella (14-16). Although this data can provide insights into long range
88 movements, spatial resolution of this data is limited, particularly in areas with poor or no mobile
89 coverage, such as forested areas (17). Alternatively, the advent of low-cost GPS tracking devices
90 allows quantification of fine-scale movements, demonstrating marked heterogeneity in individual
91 movement and risk behaviours (3, 18). Combining these data with detailed data on land cover and
92 vector dynamics can provide new insights into how landscapes affect *P. knowlesi* transmission.

93

94 Previous studies of *P. knowlesi* have relied on questionnaire surveys, identifying self-reported travel
95 to nearby plantations and forest areas as a risk factor for *P. knowlesi* and other malaria infections
96 (e.g. (19-21)). However, the resultant spatial range and frequency of these movements remain

97 unknown and the definition of different habitat types is entirely subjective. Further, little is known
98 about differences in local movement patterns in different demographic groups. While infections in
99 male adults have been linked to forest and plantation work, it is unknown whether infections
100 reported in women and young children are likely to arise from exposure to similar environments
101 (22). The main mosquito vector in this area, *An. balabacensis*, is primarily exophagic and has been
102 identified in farm, forest and village areas near houses (23, 24). Macaque populations are reported
103 in close proximity to human settlements and molecular and modelling studies suggest transmission
104 remains primarily zoonotic in this area (7, 25, 26). A case control study detected higher abundances
105 of *An. balabacensis* near *P. knowlesi* case households, suggesting the possibility of peri-domestic
106 transmission (24). Understanding the importance of these habitats is essential to effectively target
107 intervention strategies and predict impacts of future environmental changes.

108

109 Key questions remain about where individuals are likely to be exposed to *P. knowlesi* and how
110 landscape determines risk. Functional ecology approaches allow the distribution of different
111 populations to be modelled based on biological resources and relate transmission to landscape and
112 environmental factors (27). Within wildlife ecology, numerous methods have been developed to
113 estimate utilisation distributions (UDs), the probability of an individual or species being within a
114 specific location during the sampling period (28). Although these methods traditionally rely on kernel
115 density smoothing, kernel density estimates may not actually reflect time individuals spend in a
116 specific location if there is substantial missing data or irregular time intervals. Alternatively, biased
117 random bridges (BRBs) improve on these methods by estimating the utilisation distribution as a
118 time-ordered series of points, taking advantage of the autocorrelated nature of GPS tracks to bias
119 movement predictions towards subsequent locations in a time series (29). This allows for
120 interpolation of missing values and adjustment for spatial error to estimate utilisation distributions
121 representing both the intensity (mean residence time per visit) and frequency of individual visits to
122 specific locations. By integrating these estimates of individual space use with detailed spatial and

123 environmental data in a Bayesian framework, fine-scale patterns of human land use can be
124 predicted and overlaid with spatiotemporal models of mosquito distribution. This allows exploration
125 of how landscape composition, as well as configuration and connectivity between habitats, impacts
126 human exposure to *P. knowlesi* and other vector-borne and zoonotic diseases.

127

128 Focusing on one aspect of land use, human movement and time spent within different land cover
129 types, we explored the role of heterogeneity in local space use on disease exposure. Rolling cross-
130 sectional GPS tracking surveys were conducted in two study areas with on-going *P. knowlesi*
131 transmission in Northern Sabah, Malaysia (Matunggong and Limbuak (30)). We aimed to
132 characterise local movement patterns and identify individuals and locations associated with
133 increased *P. knowlesi* exposure risks by: 1. analysing individual movement patterns and developing
134 predictive maps of human space use relative to spatial and environmental factors, 2. modelling
135 biting rates of the main vector *An. balabacensis*, and 3. assessing exposure risks for *P. knowlesi*
136 based on predicted mosquito and human densities (Figure 1) Integrating these three approaches
137 allowed a uniquely spatially explicit examination of disease risk.

138

139 **Figure 1.** Analysis methods used to estimate individual and community-level exposure to *P. knowlesi*
140 sporozoite positive *An. balabacensis* bites

141

142 **Methods**

143

144 *Study site*

145 This study was conducted in two rural communities in Northern Sabah, Malaysia: Matunggong,
146 Kudat (6°47N, 116°48E, population: 1260) and Limbuak, Pulau Banggi (7°09N, 117°05E, population:
147 1009) (Figure 2). These areas were the focus for integrated entomology, primatology and social
148 science studies for risk factors for *P. knowlesi* (<https://www.lshtm.ac.uk/research/centres-projects->

149 [groups/monkeybar](#)), with clinical cases and submicroscopic infections reported from both sites and
150 *P. knowlesi* sero-prevalence estimated as 6.8% and 11.7% in Matunggong and Limbuak respectively
151 (30).

152

153 Demographic data and GPS locations of primary residences were collected for all individuals residing
154 in these areas (30). Potential spatial and environmental covariates for these sites were assembled
155 from ground-based and remote-sensing data sources (Supplementary File 1). The enhanced
156 vegetation index (EVI) was used to capture temporal changes in vegetation levels; this index
157 captures photosynthetic activity and has higher sensitivity in high biomass areas compared to the
158 normalised difference vegetation index (NDVI) frequently used. Due to the high cloud cover within
159 this area, EVI at a high spatial resolution could not be obtained for all time periods. Instead, EVI data
160 at a lower spatial but higher temporal resolution was used and monthly averages were calculated
161 from all available cloud-free data and resampled to 30m per pixel (31).

162

163 **Figure 2.** A. Location of study sites and tracked houses (households with one or more individual GPS
164 tracked) and survey houses (households with only questionnaire data collected and used for
165 prediction) in B. Matunggong, Kudat and C. Limbuak, Banggi; description of land cover classification
166 and survey methodology in (30)

167

168 *GPS tracking survey*

169 A minimum of 50 participants per site were targeted in a rolling cross-sectional survey (32). During
170 pre-defined two-week intervals, randomly selected participants from comprehensive lists of eligible
171 community members were asked to carry a QStarz BT-QT13000XT GPS tracking device (QStarz,
172 Taipei, Taiwan) programmed to record coordinates continuously at one-minute intervals for at least
173 14 days regardless of individual movement. Individuals were excluded if they were not primarily
174 residing in the study area, under 8 years old or did not consent. Trained fieldworkers visited the

175 participant every two days to confirm the device was functioning, replace batteries and administer
176 questionnaires on locations visited and GPS use. Fieldworkers recorded whether the device was
177 working and if the individual was observed carrying the GPS device to assess compliance. Individuals
178 were excluded from analysis if insufficient GPS data were collected (less than 33% of sampling
179 period) or individuals were observed not using the device for two or more visits.

180

181 *Human space use*

182 Biased random bridges were used to calculate individual utilisation distributions, the probability of
183 an individual being in a location in space within the sampled time period (29). Within this study,
184 large proportions of GPS fixes were missed due to technical issues with batteries and GPS tracking;
185 biased random bridges were used to interpolate between known locations and adjust for missing
186 data, using the time series GPS data to provide a more accurate estimate of space use. Utilisation
187 distributions were calculated separately for each individual for all movement and night-time only
188 movements (6pm – 6am).

189

190 To fit biased random bridges, we estimated the maximum threshold between points before they
191 were considered uncorrelated (T_{max}) as 3 hours based on typical reported activity times. The
192 minimum distance between relocations (L_{min}), the distance below which an individual is considered
193 stationary, was set at 10m to account for GPS recording error based on static tests. Finally, the
194 minimum smoothing parameter (h_{min}), the minimum standard deviation in relocation uncertainty,
195 was set as 30m to account for the resolution of habitat data and capture the range of locations an
196 individual could occupy while being recorded at the same place (28, 29). Estimates of the core
197 utilisation area (home range) were based on the 99th percentile, representing the area with a 99%
198 cumulative probability distribution of use by the sampled individual.

199

200 To assess relationships between space use and environmental factors and develop predictive maps
 201 of community space use, we fit resource utilisation functions, regression models in which the
 202 utilisation distributions are used as the response variable, improving on models using raw GPS count
 203 points as the response when there is location uncertainty and missing data (33). The probability
 204 density function (utilisation distribution) per individual was rasterised to 30m² grid cells and
 205 environmental and spatial covariates extracted for each grid cell. Potential environmental covariates
 206 included distance to the individual's own house, distance to closest house, distance to roads, land
 207 use class (forest, agriculture, cleared or water), distance to forest edge, elevation and slope
 208 (Supplementary File 1). Resource utilisation was modelled as a Bayesian semi-continuous (hurdle)
 209 model with two functionally independent components, a Bernoulli distribution for the probability of
 210 individual i visiting a specific grid cell j (ω_{ij}) and a gamma distribution for the utilisation distribution in
 211 grid cells visited (y_{ij}) (34, 35). For each individual, we defined absences to be all grid cells with a
 212 utilisation distribution less than 0.00001, indicating a very low probability the individual visited this
 213 grid cell during the study period. We included all presences (grid cells with a utilisation distribution >
 214 0.00001) and randomly subsampled equal numbers of absences (grid cells not visited) for each
 215 individual as including equal numbers of presences and absences can improve predictive abilities of
 216 species distribution models (36). The utilisation distribution for grid cells visited is defined as:

217

$$y_{ij} = \left\{ \begin{array}{l} \text{Gamma} \left(\frac{\mu_{ij}^2}{\sigma^2}, \frac{\sigma^2}{\mu_{ij}} \right) \text{ with probability } 1 - \phi_{ij} \\ 0 \text{ with probability } \phi_{ij} \end{array} \right\}$$

218 Where the mean of y_{ij} is given by:

$$\mu_{ij} = E(y_{ij}|X_{ij}^T) = (1 - \omega_{ij})v_{ij}$$

219 The full model was specified as:

$$\omega_{ij} \sim \text{Bernoulli}(\phi_{ij})$$

220

221

222 With the linear predictor for the Bernoulli model specified as:

223

$$\text{logit}(\phi_{ij}) = \beta_0 + X_{ij}^T \beta_i + \gamma_j$$

224

225 Where β_0 represents the intercept, $X_{ij}^T \beta_i$ represents a vector of covariate effects and γ_j represents

226 the additive terms of random effects for individual. For the Gamma component, σ^2 is the variance

227 and the linear predictor v_{ij} is specified as:

228

$$\log(v_{ij}) = \alpha_0 + X_{ij}^T \alpha_i + \varphi_j$$

229

230 With α_0 representing the intercept, $X_{ij}^T \alpha_i$ representing a vector of coordinates and φ_j representing

231 the random effects. Weakly informative normal priors specified as Normal (0,1/0.01) were used for

232 all intercepts and coefficients. Bayesian inference was implemented using integrated nested Laplace

233 approximation (INLA) (37). This approach uses a deterministic algorithm for Bayesian inference,

234 increasing computational efficiency relative to Markov chain Monte Carlo and other simulation-

235 based approaches (34). We did not explicitly include spatial autocorrelation as several distance-

236 based covariates were included (e.g. distance from own house) (33). Predictive models used data for

237 all individuals aged 8 or over residing in these communities (Table 1) and models were limited to

238 land areas within 5km of households included in the study site. Separate models were fit for each

239 site.

240

241 *Exposure to infected vectors*

242

243 To estimate vector biting rates, we assembled data from 328 nights of human landing catches (HLCs)

244 conducted with 5km of the Matunggong study site while GPS tracking was on-going, including:

245 monthly longitudinal surveillance (23), investigations surrounding households of cases and controls

246 (24), and environmentally stratified outdoor catches (38) (Supplementary File 2). We limited this
 247 data to counts of *An. balabacensis*, the primary *knowlesi* vector which comprises over 95% of
 248 *Anopheles* caught in this region. As one experiment only collected mosquitoes for 6 hours, we fit a
 249 linear model of all available data vs totals after 6 hour catches to estimate the total numbers of *An.*
 250 *balabacensis* which would have been caught over 12 hours for these data ($R^2 = 0.85$). Plausible
 251 environmental covariates were assembled, including land use type, slope, aspect, elevation,
 252 topographic wetness index, EVI, population density and average monthly temperature and rainfall.
 253 To select variables for inclusion, Pearson correlation analysis was used to assess multicollinearity
 254 between selected environmental variables. As topographic slope and TWI had a strong negative
 255 correlation, only TWI was included in the analysis. The autocorrelation function (ACF) and partial
 256 autocorrelation function (PACF) were used to explore correlation between time lags.

257

258 A Bayesian hierarchical spatiotemporal model was implemented using counts of *An. balabacensis*
 259 bites as the outcome, denoted as m_{it} ; $j = 1 \dots n$; $t = 1 \dots n$; where j indexes location and t indexes month.
 260 The log number of person-nights per catch was included as an offset to adjust for numbers of
 261 catchers conducting HLCs during different experiments. As the data were overdispersed, a negative
 262 binomial distribution was used to model m_{it} . The linear predictor was specified as:

263

$$\log(\mu_{jt}) = \log(N_{jt}) + Z_0 + D_{jt}^T Z + w_j + e_t$$

264

265 Where N_{jt} represents the number of person-nights for each HLC catch, Z_0 represents the intercept,
 266 $D_{jt}^T Z$ represents a vector of covariates, w_j is the spatial effect and e_t is the temporal effect. The
 267 temporal effect e_t was included as a fixed effect, random effect or temporally structured random
 268 walk model of order 1 in candidate models (39). The spatial effect w_j was modelled as a Matern
 269 covariance function between locations s_j and s_k :

270

$W \sim \text{Multivariate Normal}(0, \Sigma)$

$$\Sigma_{hk} = \text{Cov}(\xi(s_h), \xi(s_k)) = \text{Cov}(\xi_h, \xi_k) = \frac{\sigma^2}{\Gamma(\lambda)2^{\lambda-1}} (\kappa \|s_h - s_k\|)^\lambda K_\lambda(\kappa \|s_h - s_k\|)$$

271

272 Where $\|s_h - s_k\|$ denotes the Euclidean distance between locations s_h and s_k , $\xi(s)$ is the latent
273 Gaussian field accounting for spatial correlation, σ^2 is the spatial process variance and K_λ is a
274 modified Bessel function of the second kind and order $\lambda > 0$. κ is a scaling parameter related to r , the
275 distance at which spatial correlation becomes negligible, by $r = \sqrt{8\lambda} / \kappa$. A stochastic partial
276 differential equations (SPDE) approach was used, representing the spatial process by Gaussian
277 Markov random fields (GMRF) by partitioning the study area into non-intersecting triangles (40). This
278 approach represents the covariance matrix Σ by the inverse of the precision matrix Q of the GMRF
279 (34, 40). Prior distributions were specified on fixed effects and hyperparameters. A vague normal
280 prior distribution was used for the intercept. Weakly informative priors were used for fixed effects
281 specified as $N(1, 1/0.01)$. Priors for spatial hyperparameters were specified as range $r \sim N(10, 1/0.01)$
282 and standard deviation $\sigma \sim N(0.1, 1/0.01)$ as described by Lindgren and Rue (39).

283

284 As these vectors are rarely reported indoors (24) and HLCs were primarily conducted outside, we
285 excluded areas within houses for calculations of exposure risks. The proportion of infectious
286 mosquitoes, c , was parameterised using a beta distribution for *P. knowlesi* sporozoite rates within
287 this site; with only 4 out of 1524 collected mosquitoes positive, it was not possible to look at
288 variations of infection rates by time and space. Spatially explicit exposure risks were calculated as
289 derived quantity from human resource utilisation, mosquito biting rate models and probability of *P.*
290 *knowlesi* sporozoite positivity. Individual exposure risk was explored using a simple exposure
291 assessment model where the number of infected bites received by an individual is the sum of bites
292 by infected vector across all locations visited, with the number of infectious bites received by
293 individual i in month t as:

$$r_{it} = c \sum_{j=1}^J y_{ij} m_{jt}$$

294 Where j indexes the grid cells visited, y_{ij} is the utilisation distribution, m_{jt} is the number of bites per
 295 individual in that cell and month, and c is the proportion of infectious mosquitoes (4). To evaluate
 296 places associated with exposure for the entire community, we calculated the number of infectious
 297 bites per grid cell each month as:

$$r_{jt} = c \sum_{i=1}^I Y_{ij} m_{jt}$$

298 Where Y_{ij} is the predicted utilisation distribution for all individuals within the community per grid cell
 299 j . All analyses were conducted in R version 3.5, with Bayesian models implemented using Integrated
 300 Nested Laplace Approximation (INLA) (37). Model fit was assessed using deviance information
 301 criteria (DIC) and area under the receiver operating curve (AUC), root mean square error (RMSE) or
 302 conditional predictive ordinate (CPO) (41).

303

304 *Ethics approval*

305 This study was approved by the Medical Research Sub-Committee of the Malaysian Ministry of
 306 Health (NMRR-12-537-12568) and the Research Ethics Committee of the London School of Hygiene
 307 and Tropical Medicine (6531). Written informed consent was obtained from all participants or
 308 parents or guardians and assent obtained from children under 18.

309

310 **Results:**

311

312 Between February 2014 and May 2016, 285 consenting people participated in the GPS tracking study
 313 with 243 included in the final analysis including 109 in Limbuak and 134 in Matunggong (Table 1).
 314 The most commonly reported occupation was farm or plantation work (n=73), primarily conducted
 315 within the immediate vicinity of the house. A total of 3,424,913 GPS points were collected,

316 representing 6,319,885 person-minutes of sampling time. Median sampling duration was 16.27 days
 317 (IQR 13.72 – 19.97), with points recorded for a median of 59.1% (IQR: 46.9% - 71.1%) of the sampling
 318 duration. Maximum distances travelled ranged from no travel outside the house to 116km, with a
 319 median distance travelled of 1.8km. Utilisation distributions (UDs), the probability of an individual
 320 being in a location in space within a given time (Figure 3), varied by gender and occupation .
 321 Individuals at the more rural Limbuak site covered larger distances (Table 2), with the largest
 322 distances covered by individuals reporting primary occupations of fishing (n=5) and office work
 323 (n=9). Although substantial differences were reported in all movements (24 hour sampling) between
 324 seasons, no seasonal differences were observed in human movements during peak *Anopheles* biting
 325 times (6pm-6am).

326

327 **Table 1.** Baseline characteristics of study site communities and sampled populations

	Matunggong		Limbuak	
	Sampled	Community*	Sampled	Community*
N	134	958	109	633
Gender				
Male, % (n)	51.5% (69)	46.1% (442)	47.7% (52)	46.1% (292)
Women, % (n)	48.5% (65)	53.9% (516)	52.3% (57)	53.9% (341)
Age in years, median (IQR)	31 (17 – 53)	32.5 (8 – 51)	29 (15 – 46)	30 (15 – 47)
Main occupation, % (n)				
Farming	29.9% (40)	28.6% (274)	7.3% (8)	10.2% (65)
Plantation work	10.4% (14)	8.6% (82)	10.1% (11)	7.6% (48)
Student	26.1% (35)	27.7% (265)	26.6% (29)	21.0% (133)
Other	6.7% (9)	9.1% (87)	15.6% (17)	14.4% (91)
No employment/ housewife	26.9% (36)	26.1% (250)	40.4% (44)	46.8% (296)

328 * Community includes all individuals eligible for these surveys (residents ages 8 and over)

329

330 **Figure 3.** Human movement relative to habitat. A. Example of GPS tracks from a 22-year-old male
 331 plantation worker in Matunggong over aerial imagery, B. Probability density of an individual
 332 utilisation distribution calculated from GPS tracks

333

334 **Table 2.** Home range estimates by demographic group and site

	Area of 99% UD for all movement (hectares) Median (IQR)	Area of 99% UD from 6pm – 6am (hectares) Median (IQR)
Demographic group		
Men	32.09 (7.07, 148.93)	4.50 (2.79, 19.53)
Women	74.25 (12.24, 320.74)	6.08 (2.79, 24.17)
Children (under 15)	26.01 (6.39, 151.94)	3.83 (2.79, 8.73)
Occupation		
Farming	29.34 (8.15, 324.38)	6.75 (2.79, 19.80)
Plantation work	49.14 (9.72, 201.33)	4.59 (2.79, 27.72)
Fishing	442.49 (40.07, 1189.00)	227.16 (4.05, 465.14)
Office work	96.80 (63.61, 256.75)	13.63 (2.88, 20.14)
Other	19.98 (6.30, 26.82)	2.97 (2.61, 18.27)
No employment/ housewife	43.38 (11.97, 157.59)	3.60 (2.79, 19.12)
Site		
Limbuak	99.99 (24.57, 387.54)	7.74 (2.88, 58.05)
Matunggong	12.02 (3.94, 85.55)	2.97 (2.70, 11.77)
Season		
Dry (February – July)	28.62 (5.45, 252.45)	4.19 (2.79, 19.60)
Wet (August – January)	54.90 (17.23, 160.99)	4.64 (2.79, 19.35)

335

336

337

338 For both study areas, we developed models of community space use during peak mosquito biting
 339 hours (6pm – 6am), in the form of resource utilisation functions, predictions of time- and space-
 340 specific UD_s on the basis of spatial and environmental variables (28). Between 6pm – 6am, human
 341 space use (UD_s) was mostly predictable and negatively correlated with distance from the individual's
 342 house, other houses, roads and slope. The AUC for presence/ absence models was 0.936 for
 343 Matunggong and 0.938 for Limbuak and RMSE for the overall model was 0.0073 and 0.0043 for
 344 Matunggong and Limbuak respectively. While individuals were more likely to use areas further away
 345 from forests in the Matunggong site, human space use was positively correlated with proximity to
 346 forests in the Limbuak site (Table 3). Despite marked differences between different demographic
 347 groups and seasons observed during 24 hour movements, these factors did not improve the
 348 predictive power of the model for movements between 6pm and 6am.

349

350 **Table 3.** Estimated coefficients for fixed effects of resource utilisation functions (6pm – 6am)

	Matunggong			Limbuak		
	Mean	SD	95% CI	Mean	SD	95%CI
Probability of presence/ absence						
Intercept	3.383	0.839	3.218, 3.547	3.571	0.104	3.368, 3.775
Distance from own house (km)	-0.954	0.006	-0.966, -0.942	-0.543	0.003	-0.548, -0.539
Distance from forest (km)	5.997	0.177	-5.650, 6.344	-1.845	0.050	-1.944, -1.746
Distance from road (km)	-5.552	0.057	-5.663, -5.441	-3.656	0.019	-3.694, -3.618
Distance from houses (km)	-0.504	0.030	-0.563, -0.444	0.176	0.007	0.162, 0.189
Elevation (100 MSL)	-0.710	0.025	-0.759, -0.662	-1.268	0.037	-1.340, -1.197
Slope (degrees)	-0.0244	0.002	-0.028, -0.021	-0.009	0.001	-0.012, -0.006
Utilisation distributions for locations present						
Intercept	-6.846	0.866	-8.549, -5.147	-5.676	1.017	-7.673, -3.681
Distance from own house (km)	-0.583	0.004	-0.590, -0.576	-0.308	0.002	-0.311, -0.305
Distance from forest (km)	12.012	0.199	11.621, 12.403	-1.771	0.049	-1.868, -1.675
Distance from road (km)	-0.833	0.054	-0.939, -0.728	-1.532	0.011	-1.554, -1.511
Distance from houses (km)	-0.819	0.023	-0.864, -0.773	-0.239	0.006	-0.249, -0.228
Elevation (100 MSL)	0.664	0.027	0.610, 0.718	-0.297	0.003	-0.303, -0.297
Slope (degrees)	-0.021	0.002	-0.024, -0.018	-0.034	0.001	-0.036, -0.031

351

352 Between August 2013 and December 2015, 4814 *An. balabacensis* were caught from 328 sampling
 353 nights in 155 unique locations. The median biting rate was 2.1 bites per night per person, ranging
 354 from 0 – 28 bites per person per night (Figure 4). Despite monthly variation, including temporal
 355 autocorrelation did not improve model fit (Table 4). Although no associations were identified
 356 between land classification and vector density in this site, models identified positive relationships
 357 with enhanced vegetation indices (EVI) and negative associations with distance to forest and human
 358 population density (Table 5). Of 1524 mosquitoes tested for *Plasmodium* sporozoites, the median
 359 sporozoite rate was 0.24% (95% CI: 0.09 – 0.58%).

360

361 **Table 4.** Model selection statistics for mosquito biting rates

Model	DIC*	Marginal Likelihood	Model complexity*	RMSE*	Mean log-score (CPO)
M1 No spatial or temporal effect	2367.03	-1196.61	4.12	4.99	3.61
M2 Spatial effect only	2292.97	-1175.47	40.03	4.42	4.16
M3 Spatial effect + month as	2282.88	-1173.68	43.99	4.24	3.90

	fixed effect					
M4	Spatial effect + month as random effect	2222.89	-1155.91	50.28	4.05	3.61
M5	Spatial effect + month as random walk	2225.43	-1167.79	47.55	4.09	3.63

362

363

364 **Table 5.** Posterior rate ratio estimates and 95% Bayesian credible interval (BCI) for model 4 of
 365 mosquito biting rates

Covariate	95% BCI Rate Ratio		
	Mean	2.5%	97.5%
Population density	0.963	0.916	1.004
EVI	3.185	1.185	8.532
Distance to forest (100m)	0.926	0.871	0.976
Spatial range (km)	3.120	0.514	6.926

366

367

368 **Figure 4.** Mosquito biting rates. A. *An. balabacensis* biting rate per person-night from data collected
 369 in Matunggong, B. Predicted mean *An. balabacensis* biting rates per month from spatiotemporal
 370 models, C. Predicted number of bites for all individuals residing in Matunggong by distance from
 371 secondary forest, and by D. Distance from households

372

373

374 For individuals included in the GPS tracking study in Matunggong, where both human movement
 375 and entomology data was available, we calculated exposure risks as a derived quantity from
 376 utilisation distributions and mosquito biting rate models. Exposure varied markedly between
 377 individuals, with an overall 150-fold difference in predicted mean probabilities of infected bites per
 378 night (range: 0.00005-0.0078) (Table 6). No clear differences were observed between genders, age
 379 groups or occupations of individuals sampled and there was no association between risk and
 380 distance travelled.

381

382 **Table 6.** Probabilities of infected bites per person per night for sampled individuals in Matunggong
 383 by demographic characteristics

	Predicted infectious bites per night (median (IQR))
Demographic group	
Men	0.00157 (0.000804, 0.00289)
Women	0.00219 (0.000864, 0.00307)
Children (under 15)	0.00131 (0.000812, 0.00330)
Occupation	
Farming	0.00180 (0.00101, 0.00362)
Plantation work	0.00216 (0.000680, 0.00278)
Student	0.00143 (0.000915, 0.00304)
Other	0.00225 (0.000852, 0.00302)
No employment/ housewife	0.00142 (0.000297, 0.00263)

384

385

386 Using the resource utilisation function with demographic and spatial data for all individuals in
 387 Matunggong, we predicted community-wide space use and estimated exposure to infected
 388 mosquitoes (Figure 5). The predicted number of person nights per grid cell for the entire community
 389 ranged from 0 to 12.79 (median: 0.01, IQR: 0.0004 – 0.99), with the mean probability of a
 390 community member exposed to an infected bite per grid cell of 0.00082 (IQR: 0.00001, 0.00050).
 391 Although over 43% of the study site is forest and relatively high biting rates were predicted in forests
 392 during the study period (mean: 1.94, range: 0.04 – 12.59), this habitat was rarely used by people in
 393 the evenings, with less than 8% of predicted person-nights in forests. Models only based on
 394 mosquito biting rates and not including human space use predicted 42% of infectious bites occurred
 395 in forested areas and only 8.6% of bites occurring within 100m of houses (Figure 5C). In contrast,
 396 when space use patterns are included, over 91% of predicted infected bites were predicted within
 397 500m of houses (Figure 5D). Highest exposure risks were consistently found near forest edges and in
 398 close proximity to households, despite spatial and temporal heterogeneity and model uncertainty
 399 (Figure 4).

400

401 **Figure 5.** A. Land use in Matunggong site, B. Predicted number of person- nights for entire
402 community per grid cell, C. Predicted mosquito biting rates, D. Predicted infected bites per grid cell

403

404

405 **Discussion**

406

407 This study highlights the importance of human space use in different land cover types in determining
408 exposure to zoonotic and vector-borne diseases such as *P. knowlesi*. Although *P. knowlesi* has
409 previously been associated with forest exposure (e.g. (19)) and higher biting rates have been
410 reported in forest interiors (23), this novel approach incorporating both mosquito and human space
411 use data provides a new perspective on peri-domestic transmission, with more than 90% of
412 infectious bites predicted in areas surrounding households at forest edges. This study additionally
413 demonstrates the utility of ecological methods to understand human movement and identify
414 geographical areas associated with higher contact with disease vectors.

415

416 Within these communities, local movement patterns during peak vector times were largely
417 predictable and could be explained by spatial and environmental factors. However, despite this
418 finding, there was substantial variation in predicted exposure between individuals as a result of
419 heterogeneity in habitats used. No significant differences in exposure were predicted between men
420 and women, with individuals with high exposure risks identified across occupational and age groups.
421 Although this finding differs from clinical reports, a comprehensive survey within this community
422 identified equal proportions of men and women exposed to *P. knowlesi* as evidenced by specific
423 antibody responses and data on asymptomatic infections suggests higher numbers of non-clinical
424 infections in women (30, 42). While infrequent events or long-range movements (such as hunting
425 trips) may contribute to these differences in clinical cases and may not have been captured within

426 this two-week sampling period within the study site, this analysis highlights the importance of
427 routine movements into local environments in shaping exposure risks.

428

429 This improved understanding of how local human land use is related to exposure risk has important
430 implications for surveillance and control programmes. Malaria control programmes often rely on
431 interventions within the house, such as insecticide treated bednets and indoor residual spraying;
432 however, movements outside during peak biting times illustrate the importance of also targeting
433 outdoor transmission. The identification of areas where exposure is likely to occur can further be
434 used to refine interventions; for example, although insecticide treated hammocks have been
435 proposed for deep forest environments, larval source management may be more appropriate to
436 target environments in close proximity to houses. Although initial *P. knowlesi* cases were primarily
437 identified in adult men living and working in forests (20), this study illustrates the potential
438 importance of peri-domestic habitats in transmission and provides quantitative insight on mixing
439 between people and infected mosquitoes in forest fringe areas. As Malaysia moves towards malaria
440 elimination, surveillance systems are incorporating novel focal investigation methods, including
441 monitoring changes in local land use and populations at risk (43). In addition to routine vector
442 surveillance, this study highlights the need to incorporate measures of human space when defining
443 risk zones.

444

445 Even with the large and highly detailed movement dataset analysed, this study was limited by the
446 availability of mosquito data; as human landing catch data were assembled from other studies, there
447 was not uniform spatial and temporal coverage of the study site increasing uncertainty. The limited
448 mosquito data availability precluded development of mosquito biting rate models for Limbuak and
449 other outlying islands. An additional limitation to estimating mosquito biting rates was the difficulty
450 obtaining spatially and temporally resolute remote sensing data for predictors due to high cloud
451 cover (44). As few positive mosquitoes were identified, uniform estimates of sporozoite rates based

452 on available data were used across the Matunggong site; if further data was available, these models
453 could be refined to incorporate estimates of human and macaque density, mosquito biting
454 preferences in different habitats and infection levels in all hosts (45). Additionally, as this study was
455 designed to quantitatively estimate time spent in different landscapes, further studies could explore
456 other aspects of land use, such as the purposes of travel, activities undertaken or practices used to
457 modify or management land cover.

458

459 Despite these limitations, this is the first large-scale study to utilise GPS tracking data and ecological
460 methods to create fine-scale maps of exposure risk. This study highlights the importance of
461 incorporating heterogenous patterns of human space use into disease models, as the majority of
462 human exposure may occur in areas with lower vector biting rates but greater probabilities of
463 human use. Further, results quantitatively illustrate the importance of forest edges and local habitat
464 in *P. knowlesi* transmission and can inform understanding of other zoonotic and vector-borne
465 diseases.

466

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474

475 **Source code.** R scripts for fitting biased random bridges (with simulated GPS data), spatiotemporal
476 models of mosquito biting rates and semi-continuous resource utilisation models

477

478 **Supplementary file 1.** Data sources for assessed spatial and environmental covariates

479

480 **Supplementary file 2.** Data sources of mosquito biting data

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601

602

Human Movement

Human GPS tracks collected

- Two week sampling of randomly selected individuals (over age 8)



Biased random bridges (individual space use)

- Estimate size of area used per individual for all movements and 6pm – 6am
- Compare between individuals



Resource utilization functions (community space use)

- Identify spatial and environmental characteristics associated with increased human space use
- Develop predictive models of human space use during peak mosquito biting times



Probability of human space use during mosquito biting hours

Predicted *An. balabacensis* biting rate

Probability of infection with *P. knowlesi*

Exposure to *P. knowlesi* Number of infectious bites on humans

Mosquito Ecology

Human landing catches

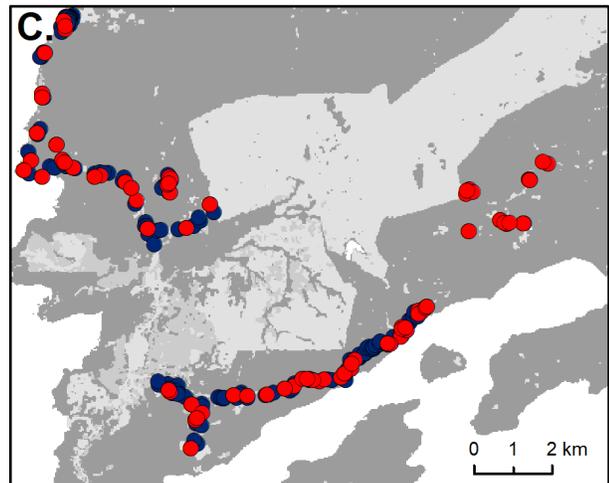
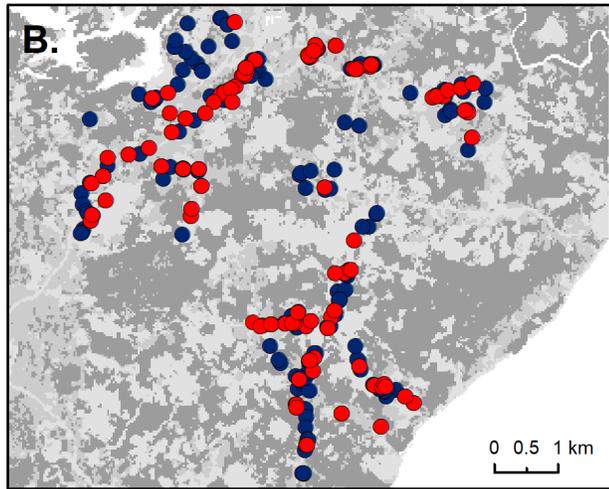
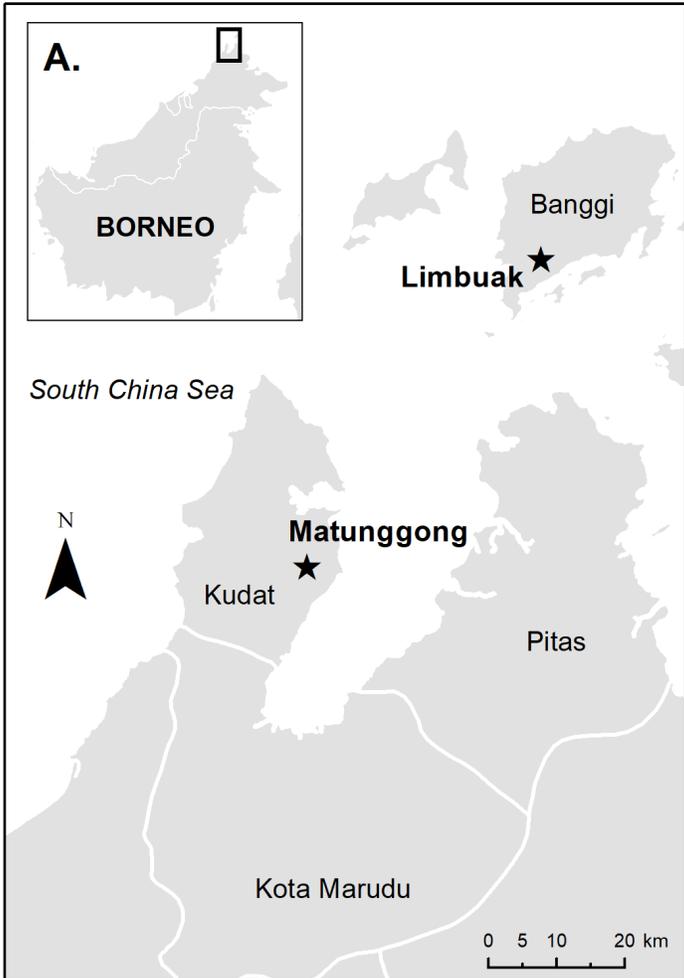
- Numbers of *An. balabacensis*
- Identification of *P. knowlesi* sporozoite positive mosquitoes

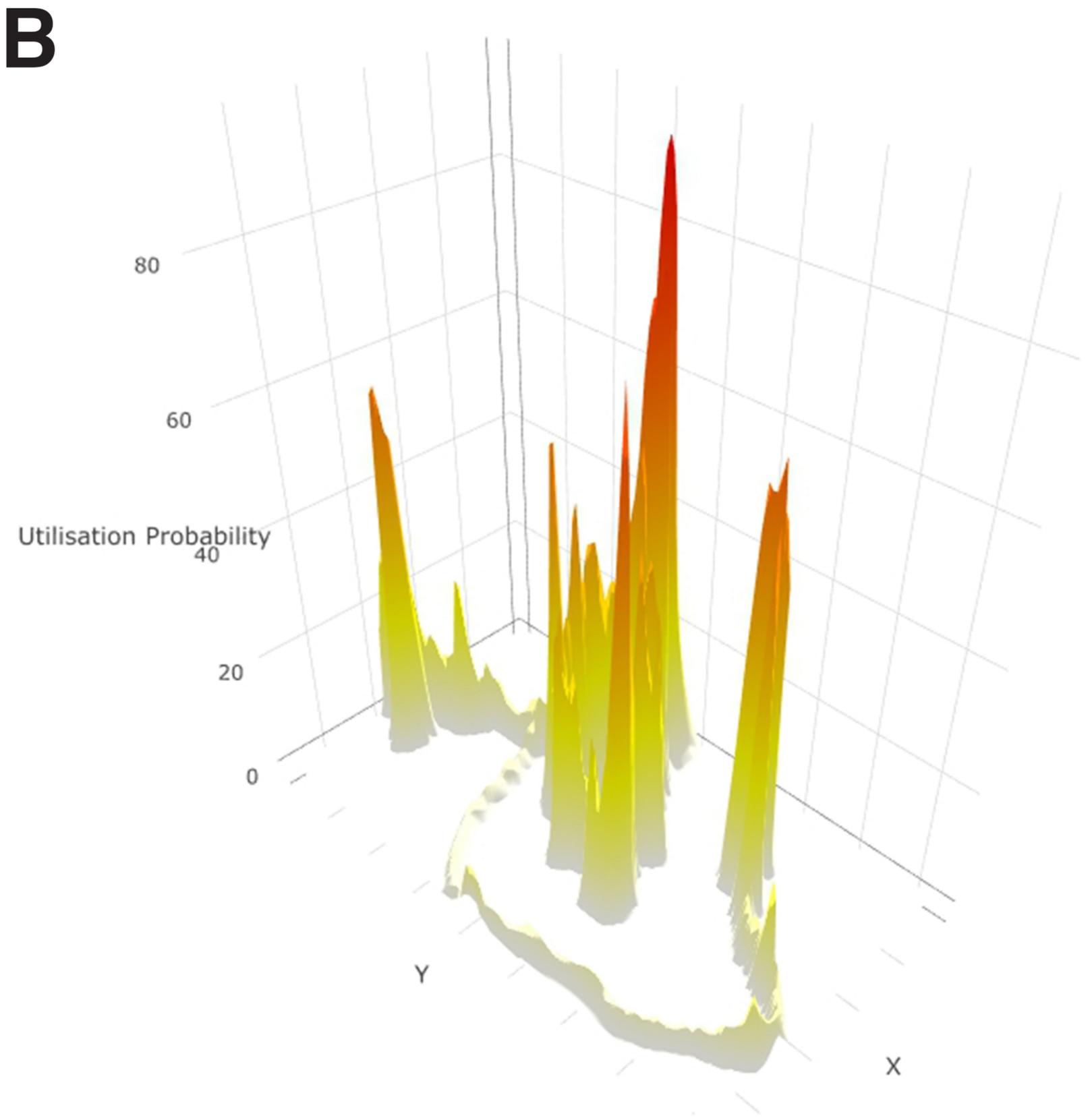
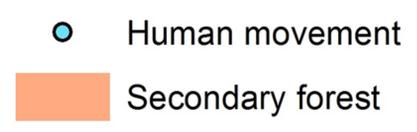
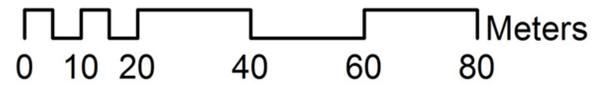
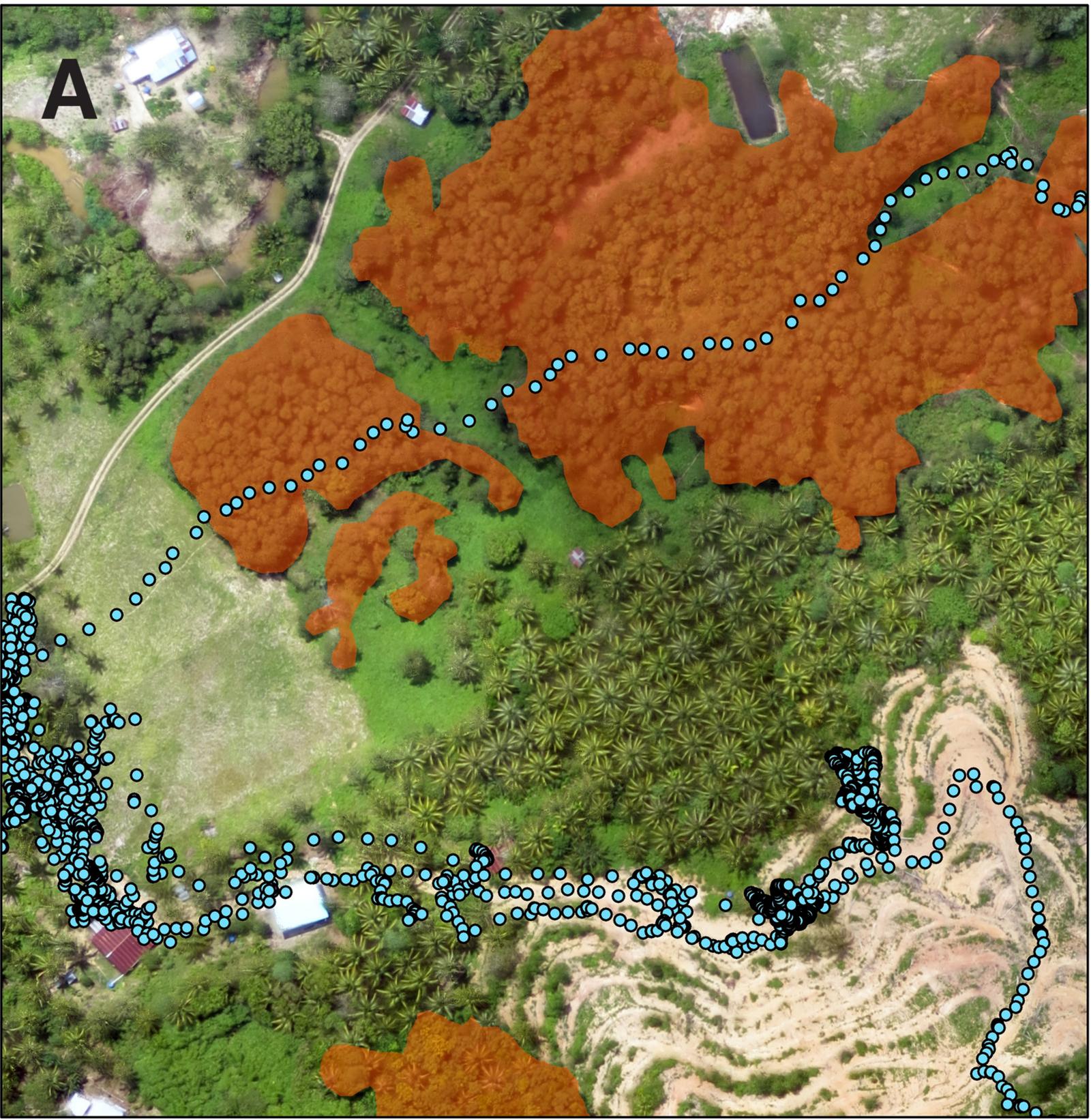


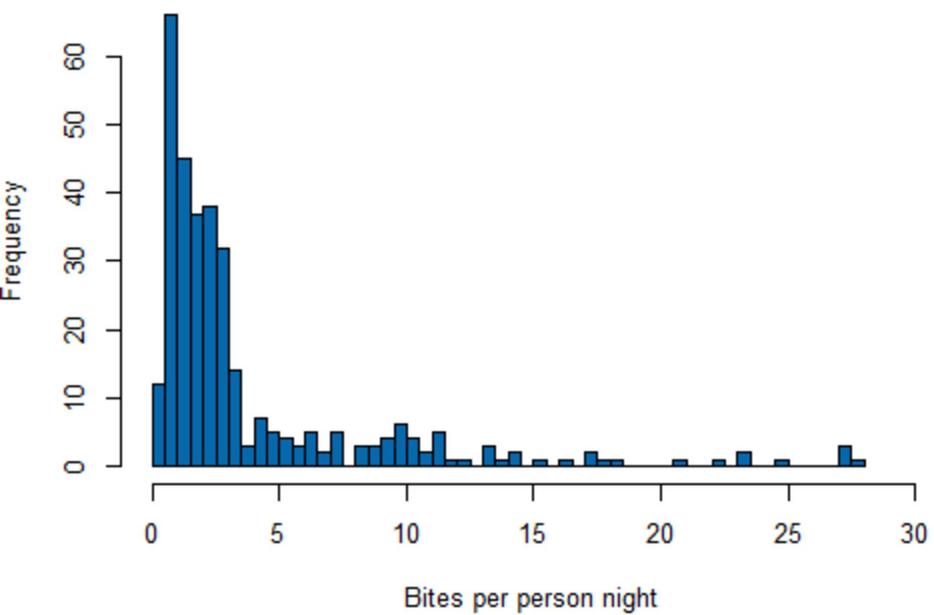
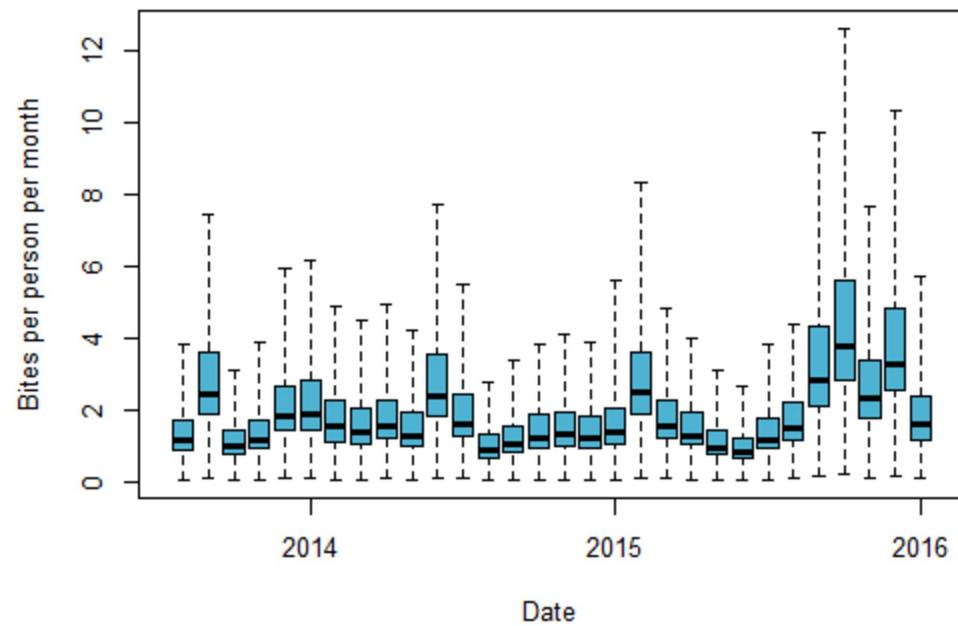
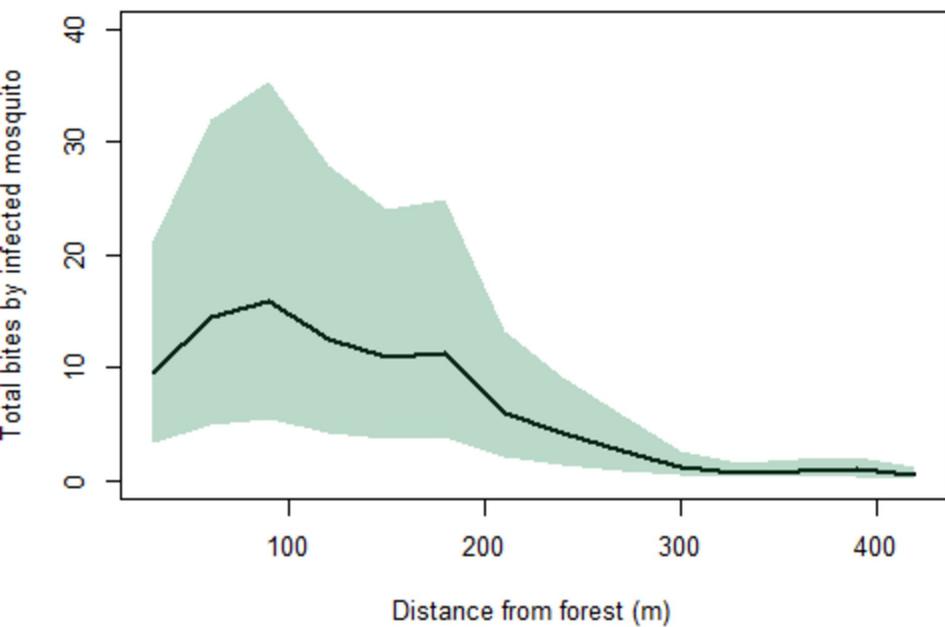
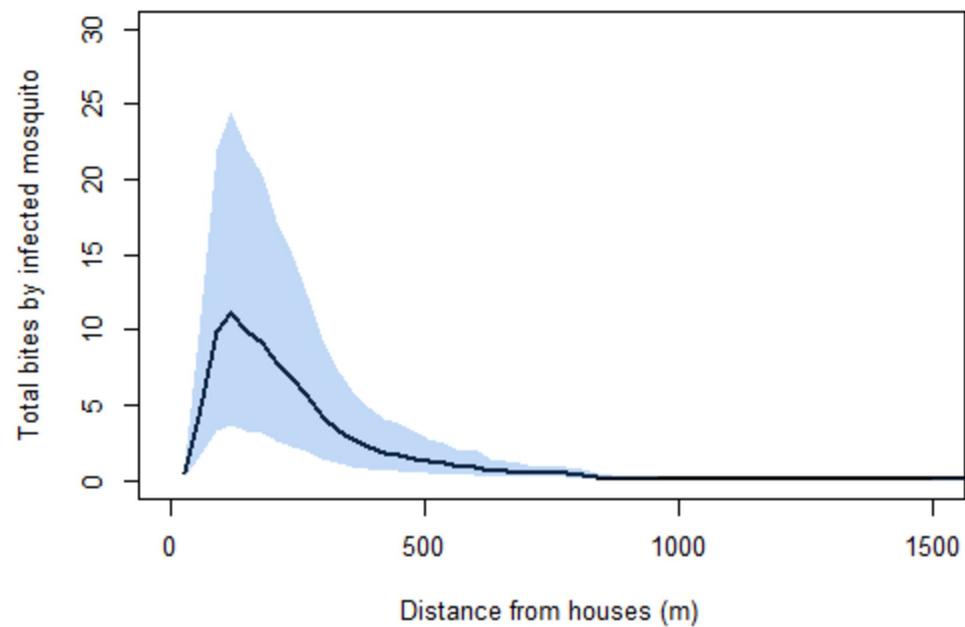
Spatiotemporal model of *An. balabacensis* biting rates

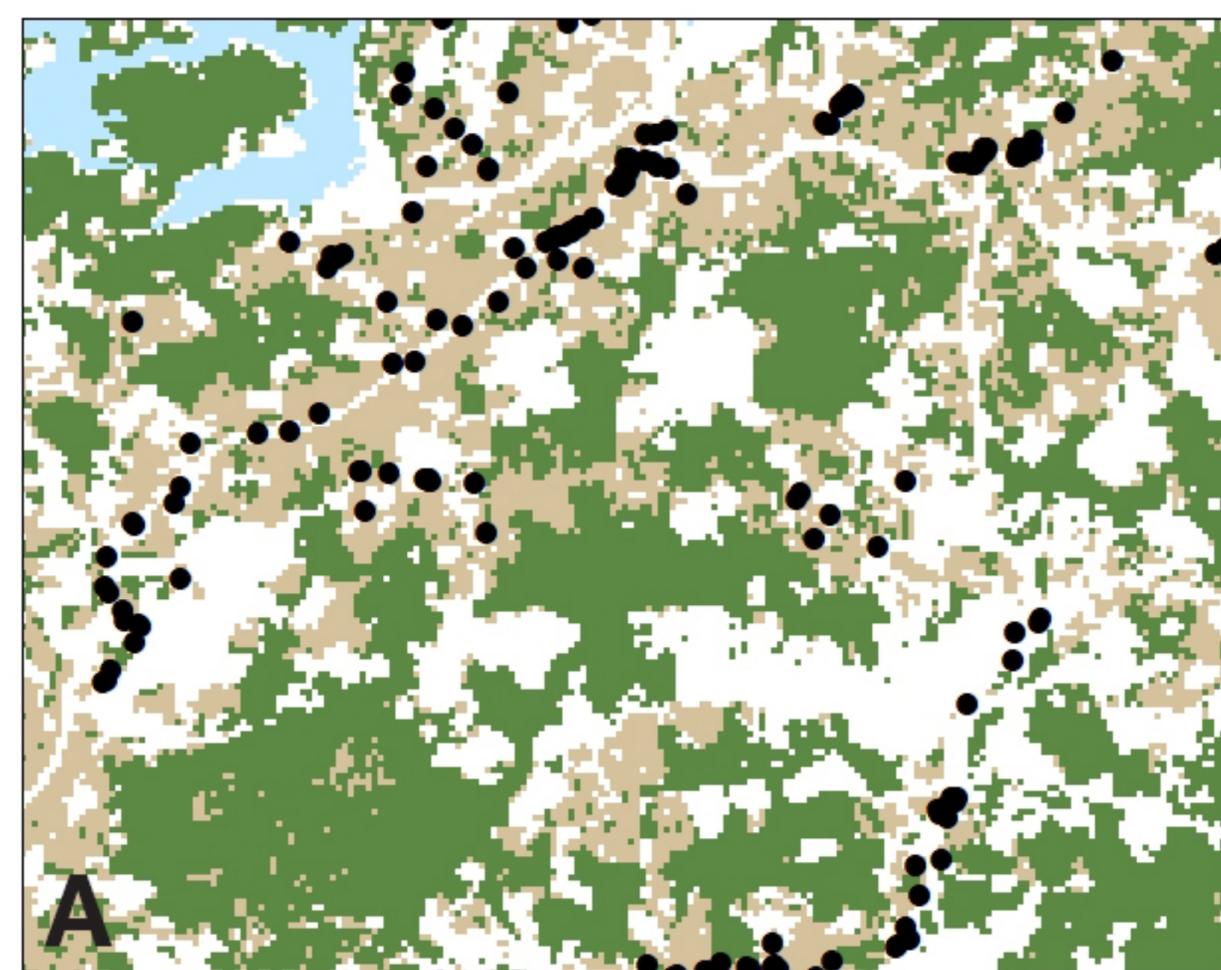
- Identify spatial and environmental factors associated with increased mosquito density
- Check residual spatial and temporal correlation
- Develop predictive model of biting rates





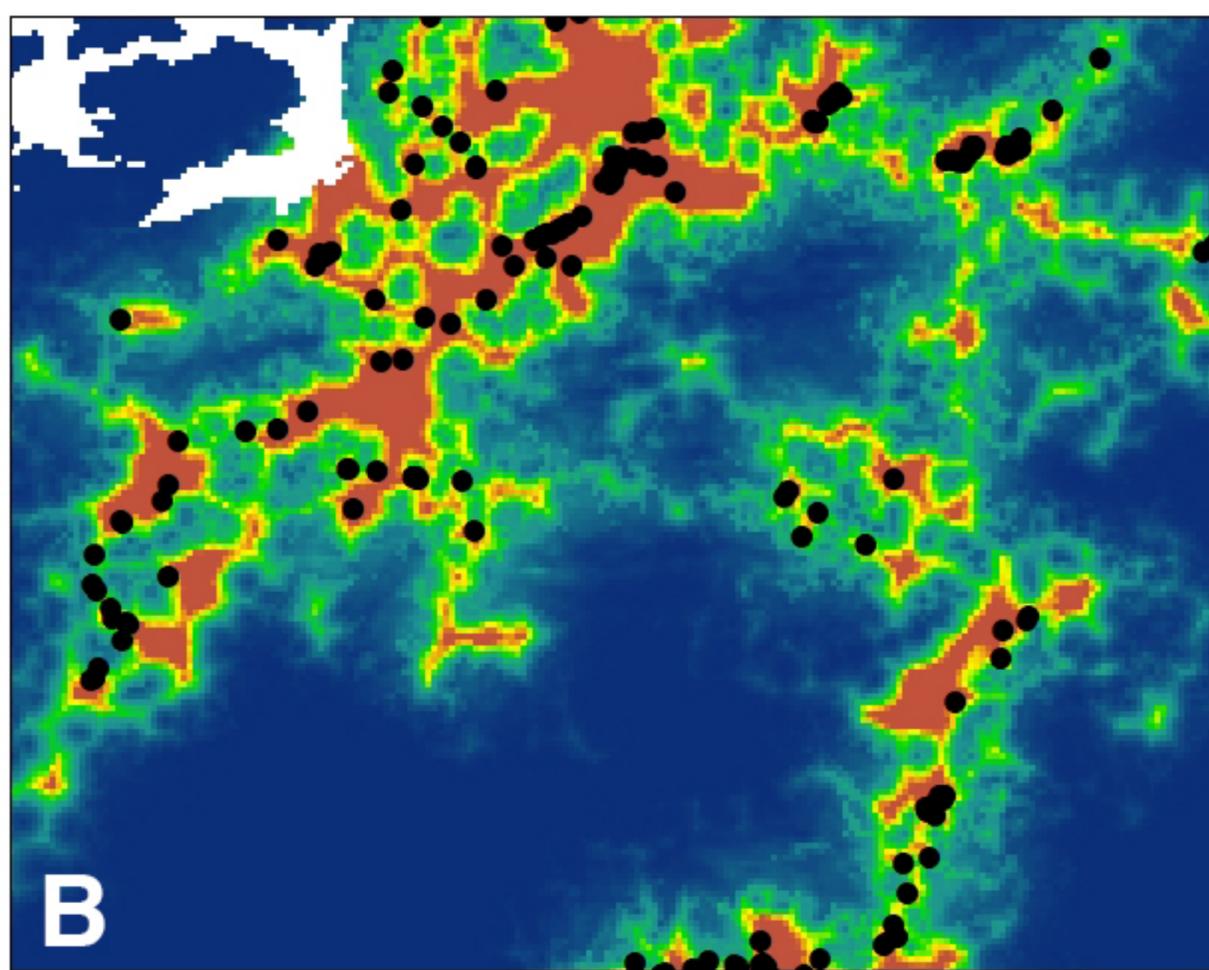


A.**B.****C.****D.**



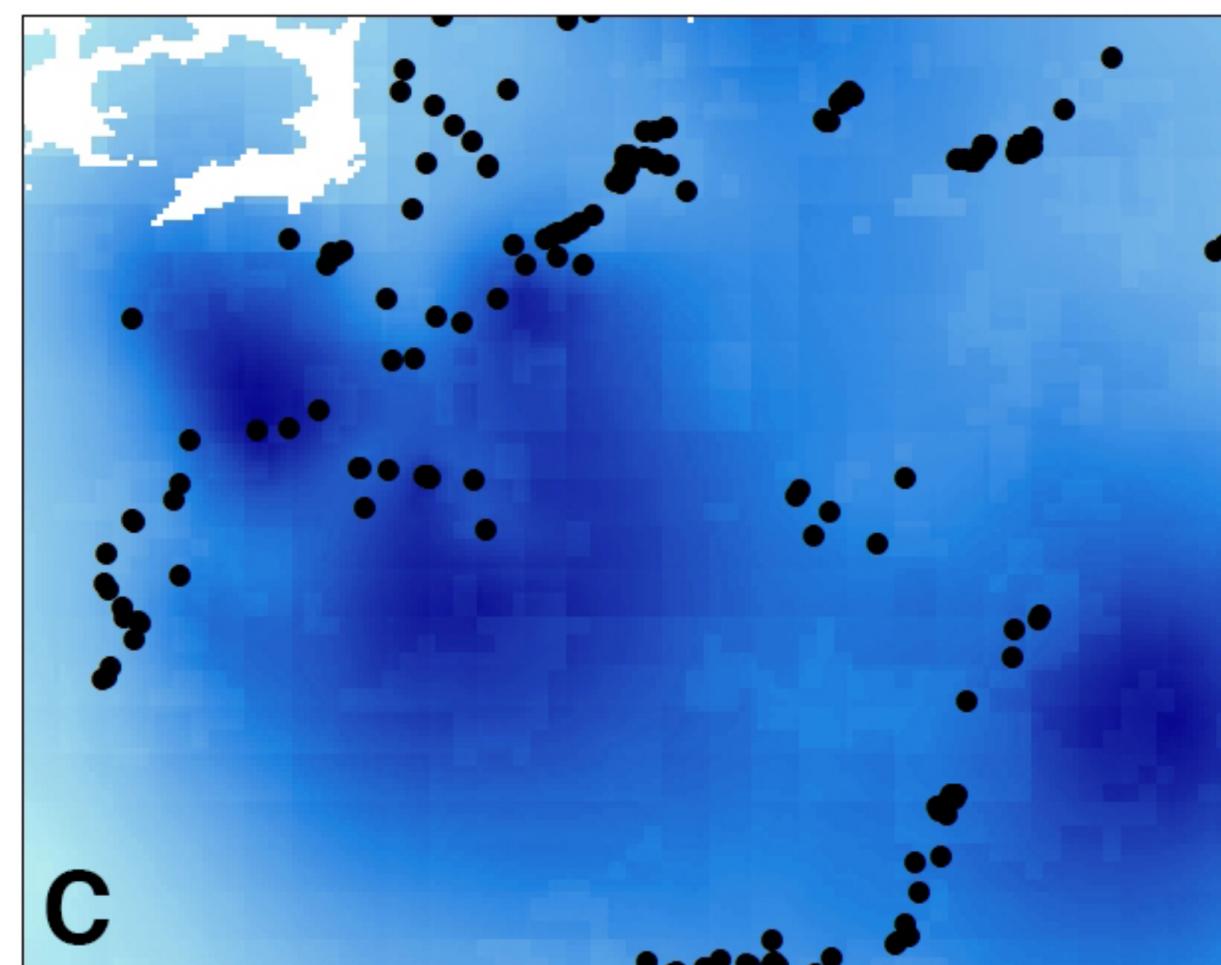
0 500 1,000 2,000 Meters

- Houses
- Forest
- Agriculture
- Clearing
- Water



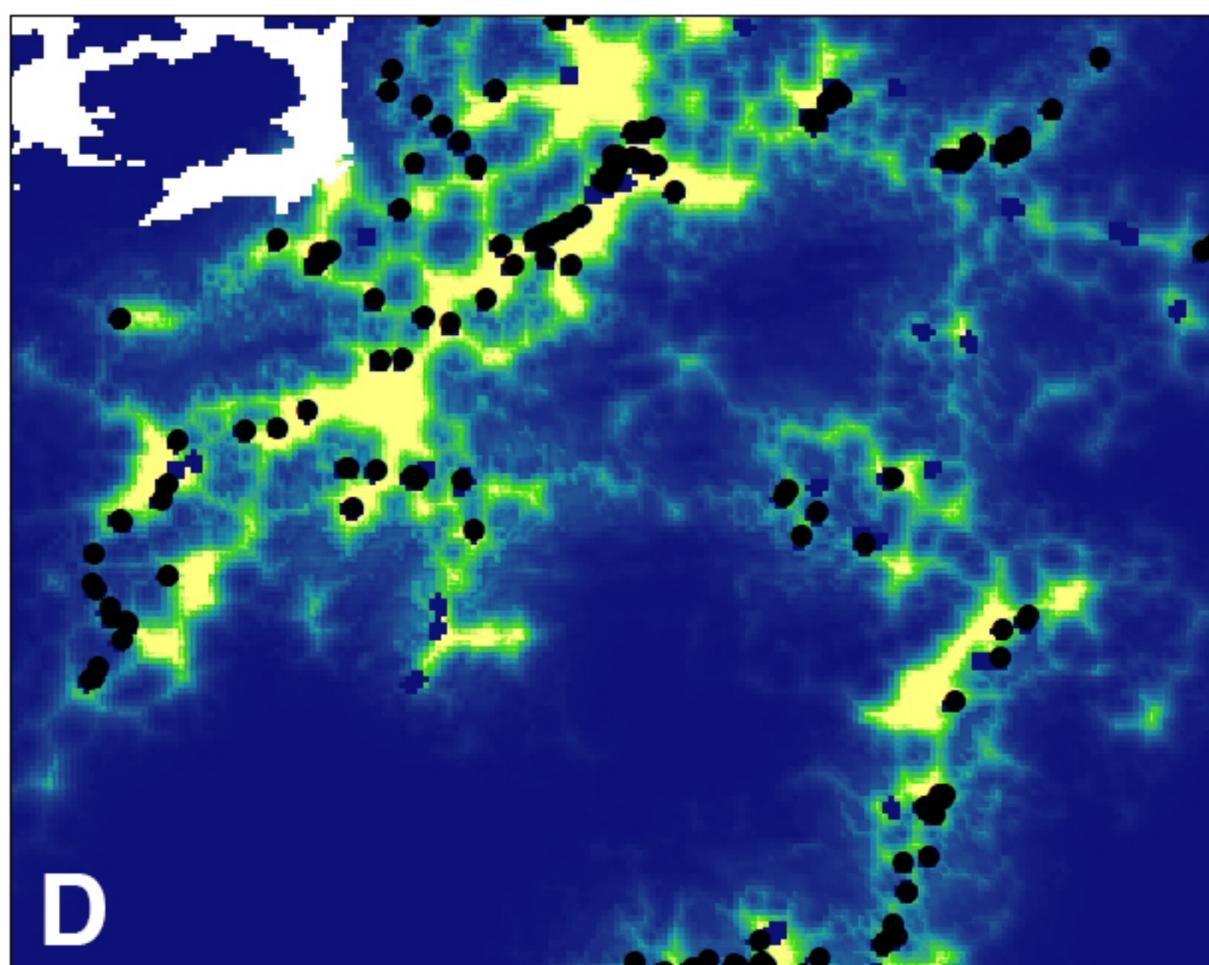
0 500 1,000 2,000 Meters

- Houses
- Total Person Nights
- High : 12.7924
- Low : 0



0 500 1,000 2,000 Meters

- Houses
- Mean biting rate
- High : 5.1001
- Low : 0.91939



0 500 1,000 2,000 Meters

- Houses
- Mean Infected Bites
- High : 0.0869811
- Low : 0