

Overlapping movements within social groups structure fine-scale heterogeneity of dengue transmission

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Appendix A. Agent-based model of dengue virus transmission

Appendix A.1. Model

The agent-based model's (ABM) description can be broken down into its constituent parts: human population structure, mosquito population structure, human-mosquito interaction, human infection, mosquito infection, circumstances surrounding the initiation of transmission, human movement, mosquito movement and time scale. It is important to note that our transmission model only concerns a single serotype of dengue, which matches infection patterns in the cluster study in Iquitos and was the impetus of this analysis (Stoddard et al., 2013).

Formally, our network of human host movements generates a weighted pseudo-digraph (Diestel, 2005) where the nodes are the houses and there are multiple directed connections going out of and into each home that are

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each weighted by the likelihood that different people visit the different homes within their contact network. Here, we allowed for nodes to be connected to themselves, corresponding to people staying at their own home. Detailed ABMs for DENV have been developed (Focks et al., 1995; Otero et al., 2011), but existing models do not allow for the types of complex human movement we are interested in evaluating. To allow us to focus on the complexity of socially structured human movement, we chose to create a new ABM that deals with virus transmission in a simple way, especially in that it simplifies the role of mosquito ecology. As mentioned in the main text, our aim was to test the viability, using a simple model, of overlapping movements within social groups as a hypothesis to explain patterns that were empirically observed in data from Iquitos, Peru (Stoddard et al., 2013).

Where possible we parameterized our model with published values from previous work on DENV transmission. We summarize parameter values used below in Table S1. In many cases, because there is a range of values across different publications, we chose ranges that are either within or encompass published values.

Appendix A.1.1. Human population structure:

On a 20-by-20 grid of houses, we placed 6 individuals into each of the 400 homes (which matches the average number of people per home in Iquitos, Peru (Stoddard et al., 2013)). Thus our simulation effort should somewhat approximate virus transmission patterns on a large neighborhood scale. There

were no births or deaths allowed for hosts, and every individual started every simulation susceptible.

Appendix A.1.2. Mosquito population structure:

Mosquito population dynamics were not explicitly simulated. The mosquito population implicitly incorporated by assigning a number of bites to each individual (described below). This results in a simplified model that doesn't allow for complexities that arise in mosquito-borne pathogen transmission when an infectious human host becomes a dead-end for transmission due to the lack of mosquitoes interacting with and/or contacting the host. We chose to have a simplified mosquito component to our ABM because our primary interest was investigating the effect of added complexity in human host movement.

Appendix A.1.3. Human-mosquito interaction:

Every time-step, at every home, each human host was assigned a number of bites received (uniformly chosen, can equal zero, this number is independent of infection status of the human host, see Table S1). Because we did not account for individual level differences in humans (such as age, sex, etc.), each individual was treated identically. Additionally, we did not incorporate time of day into the biting. As mentioned above, it was always assumed that there are enough mosquitoes in the home to accommodate the number of assigned bites. These accounted for the bites from susceptible mosquitoes, and could potentially result in an infection in a susceptible mosquito if the human host was infective. Bites from infectious mosquitoes were implicitly

included in the risk-of-infection at every house (described below).

Appendix A.1.4. Human infection:

Human infections followed a standard SEIR format (susceptible, exposed, infectious, and recovered). Every house a human visited had a risk-of-infection to humans (possibly zero). For every time-step, for every individual, a Bernoulli random variable was drawn to determine if the individual became exposed with probability of exposure equal to the risk-of-infection (see Table S1). If the individual became exposed, a length-of-incubation period and length-of-infectiousness period were randomly drawn (uniform distribution, see Table S1), and the individual was exposed for the length-of-incubation, and then infectious for the length-of-infectiousness. From that point on, the individual was immune and not susceptible to reinfection. To match the transmission patterns observed in Iquitos at the time of the empirical study (Stoddard et al., 2013), we only considered a single serotype of DENV.

Appendix A.1.5. Mosquito infection:

Mosquito infections followed a standard SEI format (susceptible, exposed and then infectious for life). If a mosquito took a blood-meal from an infectious host, there was a chance that blood-meal would result in an infection (Bernoulli distributed, see Table S1). If infection did occur, both the incubation period and the remaining lifespan of the mosquito were calculated (uniform and geometric distributions respectively). If the incubation period was longer than the remaining mosquito lifespan, nothing happened, and the mosquito died. If the remaining lifespan was longer than the incubation pe-

riod, a low, constant risk-of-infection for human hosts was temporarily added to the house's current risk-of-infection for the time the infectious mosquito lived past its incubation period. When mosquito movement was incorporated into the model (as explained below), this risk was also distributed at a fixed level to the houses adjacent to the home where the blood-meal occurred. This risk-of-infection (uniformly distributed) allowed us to account for individual infectious mosquitoes without the computational expense of explicitly tracking the life-history of the mosquito. This value was computed by tuning the simulations to allow for reasonable transmission scenarios (e.g., outbreaks can occur, they do not always, and the entire population is not infected after a few transmission cycles).

Appendix A.1.6. Circumstances surrounding the initiation of transmission:

In all simulations, transmission was initiated by the random selection of a single human and infecting them with DENV. They started their infection on day 1 at the beginning of their incubation period, transitioning into infectiousness like all other human DENV infections.

Appendix A.1.7. Human movement:

In this part of the model, we controlled for the level of overlap between different individuals within the same social group. With the limited movement of *Ae. aegypti* in mind, we considered social groups in terms of connected households. For simplicity, as explained below, we randomly assigned homes into social groups of size 6. We set each individual to visit 5 houses (excluding their home). We controlled overlap by forcing a specific number of the

locations a person visited to come from their social group (and denoted this number by κ). In Fig S1, we illustrate the grid of homes, the distribution of the homes of a representative social group (orange homes) and the movement patterns of a single individual within one of the homes of that social group for 3 different values of κ . At one extreme, people did not visit any of the other homes in their social group (other than their own home), and all of the 5 other locations they visit were randomly sampled from the remaining 394 homes in the study population (i.e., $\kappa = 0$, Fig. S1, bottom left panel). This corresponds to random and independent movement. At the other extreme, people were only allowed to visit homes within their social group (i.e., $\kappa = 5$, Fig S1, bottom right panel). This makes social groups disconnected from each other. In this circumstance, when mosquito movement was set to zero, no spread of virus transmission could ever happen on the grid because virus could never travel from one group to the next group. A moderate amount of overlap ($\kappa = 3$, Fig S1, top panel) had each individual of each social group go to two homes outside of their social group (and three homes within their social group). Our simulation study on overlap was thus reduced to investigating the effect of changing the number of houses a person visited that are in their social group from $\kappa = 0$ (resulting in only random overlaps) to $\kappa = 4$, resulting in almost perfect overlap. Note that $\kappa = 5$, as mentioned above, results in only brief transmission in the person's social group that terminates after all susceptible people in that group convert to being immune. At every time-step, people moved to one of the locations within their contact network

(including potentially the one they were currently at) by drawing from a multinomial distribution with equal weights for all non-home locations and an increased weight for their home. Matching observed patterns of movement from Iquitos (Liebman, 2012), we individually set the probability that a person moves to (or stays at) their home by drawing a random number uniformly chosen between 45% and 60%.

Appendix A.1.8. Mosquito movement:

Mosquito movement was incorporated into the model by allowing the risk that infectious mosquitoes add to their home to be instead distributed to all the houses directly adjacent to the home where the mosquito became infected as well as to the house in which they were infected. We varied the amount of risk that was distributed to the surrounding homes from 0 (i.e., no vector movement) to $1/9^{\text{th}}$ per surrounding home (corresponding to the mosquitoes uniformly visiting all the homes within 1 of the house where they were infected). This resulted in the percent of new risk that is distributed away from the home where the mosquito bit a person (and to the adjacent homes) to vary from 0 to $8/9$.

Appendix A.1.9. Time Scale:

All of the movements, interactions and bites took place with the time-step set to an hour. To account for the diurnal biting patterns of *Ae. aegypti*, each day had 12 hours.

Appendix A.1.10. Calculation of $\hat{\eta}_+$ and $\hat{\eta}_-$

The patterns in Iquitos were the results of sampling contact clusters throughout the first two years of a novel DENV serotype’s invasion. As such, herd immunity was constantly changing as the data was collected. To incorporate possible variation caused by varying population level susceptibility, we simulated the initiation of a contact study in every simulation every time the percent of the population that was susceptible dropped by 5%. When a contact study was initiated, we identified two individuals within different social groups, one who was actively infectious and one who was not. For each of these individuals, we identified the locations they had visited within the last two weeks. Then we assessed the seroconversion status of the members of each of those homes. Following the participation rates reported in Stoddard et al. (2013), each person had a 50% chance to be included in the sampling of each home. For each house, it was declared ‘infested’ if there was at least one individual with an active DENV infection. We then, for the initial infectious individual and the initial non-infectious individual, calculated the infestation rates (the percent of homes visited that were infested). Matching city-wide DENV-4 susceptible levels at the end of the empirical study, for each simulation we halted the initiation of contact studies once the percent of the population that was susceptible dropped below 75%. Finally, across 300 simulations, we averaged the average infestation rates to arrive at our estimated values of $\hat{\eta}_+$ and $\hat{\eta}_-$.

Appendix A.2. Parameter values

Below in Table S1 we give the ranges of the parameter values that govern the ABM. With the exception of the last three parameters, every value is taken from existing, relevant literature. The risk-to-infection values were chosen by calibrating the model to sustain transmission in the majority of the simulations while still allowing people to visit a house at risk and not becoming infected during every visit. The final two parameters were varied to create the different simulation scenarios. The effect of the level of overlap was evaluated by varying κ . The effect of mosquito movement was evaluated by varying the percent of the risk of infection an infectious mosquito disperses to adjacent homes.

Appendix B. Alternative model formulations

Appendix B.1. Scenarios

Appendix B.1.1. Scenario 2

In Scenario 1, we set the household size of each home equal to the mean observed in Iquitos (6 people per home). In reality the size of households varies considerably. To assess the impact of varying the household size on the metrics and conclusions drawn from Scenario 1, we implemented a new model (denoted Scenario 2) where the household size followed the distribution cited in Stoddard et al. (2013). Specifically, for every home, we drew the number of individuals residing in that home from a negative binomial distribution ($\mu = 6.2, \theta = 9.07$).

Appendix B.1.2. Scenario 3

In Scenario 1, we used the same rules to define the movement patterns of every individual. Based on data from the cluster study upon which our model is based, there was observed variation in human movement. Specifically, 15% of the population did not report moving significantly from their home. To assess the impact of heterogeneous human movement on the metrics and conclusions drawn from Scenario 1, we implemented a new model (denoted Scenario 3) where 15% of the population did not move Stoddard et al. (2013). The remaining 85% of the population's movement rules were still defined as in Scenario 1.

Appendix B.1.3. Scenario 4

In Scenario 1, we limited daily mosquito movement to directly neighboring houses. Recent work from Iquitos (Getis et al., 2003) on the abundance and spatial clustering of *Ae. aegypti* indicates that there are two spatial scales at which mosquitoes appear to cluster. First, mosquitoes cluster within 10 meters of each other, in agreement with our base simulations where mosquitoes only move one home away at a time. Second, they also found significant clustering within 30 meters, indicating the possibility of somewhat longer range dispersal. To assess the impact of increased mosquito dispersal on the metrics and conclusions drawn from Scenario 1, we implemented a new model (denoted Scenario 4) where instead of uniformly distributing the risk of mosquitoes that move to the nearest 8 homes (all homes 1 house away), we uniformly distributed this risk to the nearest 24 homes (all homes 2 houses

away).

Appendix B.1.4. Scenario 5

To assess the possibility that the heterogeneities have significant non-linear interactions, we combined the variants incorporated in scenario 2-4 into a single scenario. Scenario 5 allowed for varying household size, heterogeneous human movement and extended mosquito movement.

Appendix B.2. Results

The results for scenario 2 (Figs. S3, S4), 3 (Figs. S5, S6), 4 (Figs. S7, S8), and 5 (Figs. S9, S10) agree with those from Scenario 1. Specifically, when human movement was highly structured and mosquito movement was present but weak, the empirical patterns were recreated (Fig S3, S5, S7, S9). Further, as with Scenario 1, when mosquito movement was completely removed from the model, the signature of structure human movement was clearly visible within spatially aggregated weekly incidence curves. Also in concordance, when mosquito movement was reintroduced, the strength of structured human movement was not easily determinable from the aggregated epidemic curves (Fig S4, S6, S8, S10).

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Figure S1. **Socially structured movements among households.** On a grid of 20 x 20 homes, we conducted our simulation experiments by enforcing varying levels of structure on human movements within and without social groups. In all simulations, every house was a member of a social group of 6 homes. Additionally, every individual of every home visited 6 homes.

b. At one extreme (bottom right panel, $\kappa = 0$), no individual of any social group visited any home within their social group. This corresponds to random movement patterns for each individual.

c. At the other extreme (bottom left panel, $\kappa = 5$), individuals only moved to homes within their social group, effectively isolating each social group from each other. In this case only mosquitoes bridged social groups by traveling to adjacent homes that were members of different groups and DENV transmission stalls.

a. A moderate amount of structure on individual movement (top panel, $\kappa = 3$), allowed for movement both within and without an individual's social group.

Figure S2. **Hidden heterogeneity, scenario 1.** 5th percentile (left panel), median (middle panel) and 95th percentile (right panel) for weekly incidence curves of DENV for scenario 1 with varying levels of mosquito movement. The percent of people that visited a home outside their social group varies from 10% (dark red, corresponding to $\kappa = 4.9$) to 100% (dark green, corresponding to $\kappa = 4$).

(a) 0% mosquito movement, (b) 11% mosquito movement, (c) 22% mosquito movement, (d) 33% mosquito movement, (e) 44% mosquito movement, (f) 55% mosquito movement, (g) 66% mosquito move-

ment, (h) 77% mosquito movement, (i) 88% mosquito movement.

Figure S3: **Pattern matching ($\bar{\eta}_+$ and $\bar{\eta}_-$) of simulation results, scenario 2.** a. Left panel: Values of $\bar{\eta}_+$ (top, red surface, the percent of homes in a DENV positive cluster that contained at least one concurrently infectious person) and $\bar{\eta}_-$ (bottom, dark blue surface, the percent of homes in a DENV negative cluster that contained at least one concurrently infectious person) across different values of mosquito movement and κ (the number of homes and individual visits, excluding their own, that come from their social group). The empirical values observed in Iquitos are given by the orange and light blue surfaces for the DENV positive and DENV negative clusters, respectively. b. Right panel: The dark red and dark blue lines indicate where the simulated surfaces intersect with the empirically observed values for DENV positive and DENV negative clusters respectively. To incorporate some uncertainty in the empirically observed values, we found what values of mosquito movement and κ corresponded with simulated values "close" to those observed in Iquitos (where close is within 2.5%). The purple shaded region corresponds to combination of mosquito movement and κ that closely approximated the empirical patterns found in Iquitos.

Figure S4. **Hidden heterogeneity, scenario 2.** 5th percentile (left panel), median (middle panel) and 95th percentile (right panel) for weekly incidence curves of DENV for scenario 2 with varying levels of mosquito movement.

The percent of people that visited a home outside their social group varies from 10% (dark red, corresponding to $\kappa = 4.9$) to 100% (dark green, corresponding to $\kappa = 4$). (a) 0% mosquito movement, (b) 11% mosquito movement, (c) 22% mosquito movement, (d) 33% mosquito movement, (e) 44% mosquito movement, (f) 55% mosquito movement, (g) 66% mosquito movement, (h) 77% mosquito movement, (i) 88% mosquito movement.

Figure S5: **Pattern matching ($\bar{\eta}_+$ and $\bar{\eta}_-$) of simulation results, scenario 3.** a. Left panel: Values of $\bar{\eta}_+$ (top, red surface, the percent of homes in a DENV positive cluster that contained at least one concurrently infectious person) and $\bar{\eta}_-$ (bottom, dark blue surface, the percent of homes in a DENV negative cluster that contained at least one concurrently infectious person) across different values of mosquito movement and κ (the number of homes and individual visits, excluding their own, that come from their social group). The empirical values observed in Iquitos are given by the orange and light blue surfaces for the DENV positive and DENV negative clusters, respectively. b. Right panel: The dark red and dark blue lines indicate where the simulated surfaces intersect with the empirically observed values for DENV positive and DENV negative clusters respectively. To incorporate some uncertainty in the empirically observed values, we found what values of mosquito movement and κ corresponded with simulated values "close" to those observed in Iquitos (where close is within 2.5%). The purple shaded region corresponds to combination of mosquito movement and κ that closely

approximated the empirical patterns found in Iquitos.

Figure S6. **Hidden heterogeneity, scenario 3.** 5th percentile (left panel), median (middle panel) and 95th percentile (right panel) for weekly incidence curves of DENV for scenario 3 with varying levels of mosquito movement. The percent of people that visited a home outside their social group varies from 10% (dark red, corresponding to $\kappa = 4.9$) to 100% (dark green, corresponding to $\kappa = 4$). (a) 0% mosquito movement, (b) 11% mosquito movement, (c) 22% mosquito movement, (d) 33% mosquito movement, (e) 44% mosquito movement, (f) 55% mosquito movement, (g) 66% mosquito movement, (h) 77% mosquito movement, (i) 88% mosquito movement.

Figure S7: **Pattern matching ($\bar{\eta}_+$ and $\bar{\eta}_-$) of simulation results, scenario 4.** a. Left panel: Values of $\bar{\eta}_+$ (top, red surface, the percent of homes in a DENV positive cluster that contained at least one concurrently infectious person) and $\bar{\eta}_-$ (bottom, dark blue surface, the percent of homes in a DENV negative cluster that contained at least one concurrently infectious person) across different values of mosquito movement and κ (the number of homes and individual visits, excluding their own, that come from their social group). The empirical values observed in Iquitos are given by the orange and light blue surfaces for the DENV positive and DENV negative clusters, respectively. b. Right panel: The dark red and dark blue lines indicate where the simulated surfaces intersect with the empirically observed values

for DENV positive and DENV negative clusters respectively. To incorporate some uncertainty in the empirically observed values, we found what values of mosquito movement and κ corresponded with simulated values "close" to those observed in Iquitos (where close is within 2.5%). The purple shaded region corresponds to combination of mosquito movement and κ that closely approximated the empirical patterns found in Iquitos.

Figure S8. **Hidden heterogeneity, scenario 4.** 5th percentile (left panel), median (middle panel) and 95th percentile (right panel) for weekly incidence curves of DENV for scenario 4 with varying levels of mosquito movement. The percent of people that visited a home outside their social group varies from 10% (dark red, corresponding to $\kappa = 4.9$) to 100% (dark green, corresponding to $\kappa = 4$). (a) 0% mosquito movement, (b) 11% mosquito movement, (c) 22% mosquito movement, (d) 33% mosquito movement, (e) 44% mosquito movement, (f) 55% mosquito movement, (g) 66% mosquito movement, (h) 77% mosquito movement, (i) 88% mosquito movement.

Figure S9: **Pattern matching ($\bar{\eta}_+$ and $\bar{\eta}_-$) of simulation results, scenario 5.** a. Left panel: Values of $\bar{\eta}_+$ (top, red surface, the percent of homes in a DENV positive cluster that contained at least one concurrently infectious person) and $\bar{\eta}_-$ (bottom, dark blue surface, the percent of homes in a DENV negative cluster that contained at least one concurrently infectious person) across different values of mosquito movement and κ (the number of

homes and individual visits, excluding their own, that come from their social group). The empirical values observed in Iquitos are given by the orange and light blue surfaces for the DENV positive and DENV negative clusters, respectively. b. Right panel: The dark red and dark blue lines indicate where the simulated surfaces intersect with the empirically observed values for DENV positive and DENV negative clusters respectively. To incorporate some uncertainty in the empirically observed values, we found what values of mosquito movement and κ corresponded with simulated values "close" to those observed in Iquitos (where close is within 2.5%). The purple shaded region corresponds to combination of mosquito movement and κ that closely approximated the empirical patterns found in Iquitos.

Figure S10. **Hidden heterogeneity, scenario 5.** 5th percentile (left panel), median (middle panel) and 95th percentile (right panel) for weekly incidence curves of DENV for scenario 5 with varying levels of mosquito movement. The percent of people that visited a home outside their social group varies from 10% (dark red, corresponding to $\kappa = 4.9$) to 100% (dark green, corresponding to $\kappa = 4$). (a) 0% mosquito movement, (b) 11% mosquito movement, (c) 22% mosquito movement, (d) 33% mosquito movement, (e) 44% mosquito movement, (f) 55% mosquito movement, (g) 66% mosquito movement, (h) 77% mosquito movement, (i) 88% mosquito movement.

Table B.1: Parameter values used in ABM of DENV transmission

Parameter	Range of values	Published value or range and reference
Human DENV incubation period (days, uniform distribution)	(4,7)	(4-5) (Gubler and Kuno, 1997), (4.5 - 7) (Siler et al., 1926), (Normal with mean 5.5 and deviation 1.5 i.e. $N(5.5,1.5)$) (de Castro Medeiros et al., 2011), (4) (Focks et al., 1995), (5) (Newton and Reiter, 1992)
Human DENV infectious period (days, uniform distribution)	(4,5)	(4-5) (Gubler et al., 1981), (5) (Otero et al., 2011), (3-5) (Favier et al., 2005), $N(4.5,1.5)$ (de Castro Medeiros et al., 2011), (3)(Newton and Reiter, 1992)
Human-to-mosquito DENV transmission probability (uniform distribution)	(0.5,0.75)	(.25-1) (Otero et al., 2011), (.1-1) (Focks et al., 1995), (.75) (Newton and Reiter, 1992)
Mosquito DENV incubation period (days uniform distribution)	(8,10)	(8) (Otero et al., 2011), (7-12) (Favier et al., 2005), $N(9,0.25)$, (5-40 (temp dependent, 12.5 at 25 degrees)) (Focks et al., 1995), (10) (Newton and Reiter, 1992)
Mosquito DENV lifespan mean (days, uniform distribution). This value was then used as the mean of a geometric random variable to determine the individual mosquito's lifespan.	(10,18)	(8-15) (Gubler and Kuno, 1997), (11) (Otero et al., 2008), (1/.11 w/senescence) (Magori et al., 2009)
Bites per host per hour (uniform distribution)	(0,4)	NA
Risk-of-infection	(0.0001,0.001)	NA
κ	(1,5)	NA
Percent of risk from infectious vectors distributed evenly to all adjacent homes (deterministically varied across scenarios)	(0,8/9)	NA