SUPPLEMENTARY MATERIAL: A MECHANISTIC MODEL TO COMPARE THE IMPORTANCE OF INTERRELATED POPULATION MEASURES: HOST POPULATION SIZE, DENSITY AND COLONY SIZE

TIM LUCAS, HILDE HERBOTS AND KATE JONES

S1. Supplementary methods

S1.1. **Stochastic simulations.** We examined the model using stochastic, continuous-time simulations implemented in *R* [1]. The implementation is available as an *R* package on GitHub [2]. The model can be written as a continuous-time Markov chain. The Markov chain contains the random variables $((S_x)_{x=1\dots m}, (I_{x,q})_{x=1\dots m,\, q\in\{1,2,12\}}, (R_x)_{x=1\dots m})$. Here, $(S_x)_{x=1\dots m}$ is a length m vector of the number of susceptibles in each colony. $(I_{x,q})_{x=1\dots m, q\in\{1,2,12\}}$ is a length $m \times 3$ vector describing the number of individuals of each disease class ($q \in \{1, 2, 12\}$) in each colony. Finally, $(R_x)_{x=1\dots m}$ is a length m vector of the number of individuals in the recovered class. The model is a Markov chain where extinction of both pathogen species and extinction of the host species are absorbing states. The expected time for either host to go extinct is much larger than the duration of the simulations.

At any time, suppose the system is in state $((s_x), (i_{x,q}), (r_x))$. At each step in the simulation we calculate the rate at which each possible event might occur. One event is then randomly chosen, weighted by its rate

$$p(\text{event } i) = \frac{e_i}{\sum_j e_j}, \tag{1}$$

where e_i is the rate at which event i occurs and $\sum_j e_j$ is the sum of the rates of all possible events. Finally, the length of the time step, δ, is drawn from an exponential distribution

$$\delta \sim \text{Exp}\left(\sum_j e_j\right). \tag{2}$$

We can now write down the rates of all events. Assuming asexual reproduction, that all classes reproduce at the same rate and that individuals are born into the susceptible class we get

$$s_x \to s_x + 1 \quad \text{at a rate of } \Lambda\left(s_x + \sum_q i_{qx} + r_x\right) \tag{3}$$

where $s_x \to s_x + 1$ is the event that the number of susceptibles in colony x will increase by 1 (a single birth) and $\sum_q i_{qx}$ is the sum of all infection classes $q \in \{1, 2, 12\}$. The rates of death, given a death rate μ, and no increased mortality due to infection, are given by

$$s_x \to s_x - 1 \quad \text{at a rate of } \mu s_x, \tag{4}$$
$$i_{qx} \to i_{qx} - 1 \quad \text{at a rate of } \mu i_{qx}, \tag{5}$$
$$r_x \to r_x - 1 \quad \text{at a rate of } \mu r_x. \tag{6}$$

We modelled transmission as being density-dependent. This assumption was more suitable than frequency-dependent transmission as we were modelling a disease transmitted by saliva or urine in highly dense populations confined to caves, buildings or potentially a small number of tree roosts. We were notably not modelling a sexually transmitted disease (STD) as spillover of STDs from bats to humans is likely to be rare. Infection of a susceptible with either Pathogen 1 or 2 is therefore given by

$$i_{1x} \to i_{1x} + 1, \quad s_x \to s_x - 1 \ \text{ at a rate of } \beta s_x\left(i_{1x} + i_{12x}\right), \tag{7}$$
$$i_{2x} \to i_{2x} + 1, \quad s_x \to s_x - 1 \ \text{ at a rate of } \beta s_x\left(i_{2x} + i_{12x}\right), \tag{8}$$

while coinfection, given the coinfection adjustment factor α, is given by

$$i_{12,x} \to i_{12,x} + 1, \quad i_{1x} \to i_{1x} - 1 \ \text{ at a rate of } \alpha\beta i_{1x}\left(i_{2x} + i_{12x}\right), \tag{9}$$
$$i_{12,x} \to i_{12,x} + 1, \quad i_{2x} \to i_{2x} - 1 \ \text{ at a rate of } \alpha\beta i_{2x}\left(i_{1x} + i_{12x}\right). \tag{10}$$

Note that lower values of α give lower rates of coinfection as in Castillo-Chavez et al. [3].

The rate of migration from colony y (with degree k_y) to colony x, given a dispersal rate ξ is given by

$$s_x \to s_x + 1, \quad s_y \to s_y - 1 \text{ at a rate of } \frac{\xi s_y}{k_y}, \tag{11}$$

$$i_{qx} \to i_{qx} + 1, \quad i_{qy} \to i_{qy} - 1 \text{ at a rate of } \frac{\xi i_{qy}}{k_y}, \tag{12}$$

$$r_x \to r_x + 1, \quad r_y \to r_y - 1 \text{ at a rate of } \frac{\xi r_y}{k_y}. \tag{13}$$

Note that the dispersal rate does not change with infection. As above, this is due to the low virulence of bat viruses. Finally, recovery from any infectious class occurs at a rate γ

$$i_{qx} \to i_{qx} - 1, \;\; r_x \to r_x + 1 \text{ at a rate of } \gamma i_{qx}. \tag{14}$$

S2. Supplementary results

TABLE S1. A summary of all symbols used along with their units and default values. The justifications for parameter values are given in the main manuscript.

Symbol	Explanation	Units	Value
ρ	Number of pathogens		2
x, y	Colony index		
p	Pathogen index i.e. $p \in \{1, 2\}$ for pathogens 1 and 2		
q	Disease class i.e. $q \in \{1, 2, 12\}$		
S_x	Number of susceptible individuals in colony x		
I_{qx}	Number of individuals infected with disease(s) $q \in \{1, 2, 12\}$ in colony x		
R_x	Number of individuals in colony x in the recovered with immunity class		
N	Total Population size		30,000
m	Number of colonies		10
n	Colony size		3,000
a	Area	km^2	10,000
β	Transmission rate		0.1 – 0.4
α	Coinfection adjustment factor		0.1
γ	Recovery rate	$year^{-1}.individual^{-1}$	1
ξ	Dispersal rate	$year^{-1}.individual^{-1}$	0.001–0.1
Λ	Birth rate	$year^{-1}.individual^{-1}$	0.05
μ	Death rate	$year^{-1}.individual^{-1}$	0.05
k_x	Degree of node x (number of colonies that individuals from colony x can disperse to).		
δ	Waiting time until next event	years	
e_i	The rate at which event i occurs	$year^{-1}$	

TABLE S2. Raw data for range size simulations. The population parameters are shown along with the number of invasions and the number of simulations. Note that simulations where both pathogens went extinct have been removed (100 simulations were originally run for each parameter set). β is the transmission rate, n is colony size, m is the number of colonies and N is the total population size.

β	n	m	Area ($\times 1000$ km^2)	N ($\times 1000$)	Density (km^{-2})	Invasions	Sims
0.1	400	20	2.5	8	3.2	2	100
0.1	400	20	5.0	8	1.6	3	100
0.1	400	20	10.0	8	0.8	2	100
0.1	400	20	20.0	8	0.4	3	100
0.1	400	20	40.0	8	0.2	2	100
0.2	400	20	2.5	8	3.2	3	100
0.2	400	20	5.0	8	1.6	3	100
0.2	400	20	10.0	8	0.8	1	100
0.2	400	20	20.0	8	0.4	4	100
0.2	400	20	40.0	8	0.2	1	100
0.3	400	20	2.5	8	3.2	3	100
0.3	400	20	5.0	8	1.6	3	100
0.3	400	20	10.0	8	0.8	3	100
0.3	400	20	20.0	8	0.4	5	100
0.3	400	20	40.0	8	0.2	9	100

Table S3. Raw data for colony size simulations. The population parameters are shown along with the number of invasions and the number of simulations. Note that simulations where both pathogens went extinct have been removed (100 simulations were originally run for each parameter set). β is the transmission rate, n is colony size, m is the number of colonies and N is the total population size.

β	n	m	Area ($\times 1000$ km^2)	N ($\times 1000$)	Density (km^{-2})	Invasions	Sims
0.1	100	20	2.5	2	0.8	4	88
0.1	200	20	5.0	4	0.8	5	100
0.1	400	20	10.0	8	0.8	2	100
0.1	800	20	20.0	16	0.8	0	100
0.1	1600	20	40.0	32	0.8	55	100
0.2	100	20	2.5	2	0.8	3	92
0.2	200	20	5.0	4	0.8	6	100
0.2	400	20	10.0	8	0.8	0	100
0.2	800	20	20.0	16	0.8	39	100
0.2	1600	20	40.0	32	0.8	95	100
0.3	100	20	2.5	2	0.8	1	91
0.3	200	20	5.0	4	0.8	4	100
0.3	400	20	10.0	8	0.8	7	100
0.3	800	20	20.0	16	0.8	67	100
0.3	1600	20	40.0	32	0.8	100	100

Table S4. Raw data for number of colonies simulations. The population parameters are shown along with the number of invasions and the number of simulations. Note that simulations where both pathogens went extinct have been removed (100 simulations were originally run for each parameter set). β is the transmission rate, n is colony size, m is the number of colonies and N is the total population size.

β	n	m	Area ($\times 1000$ km^2)	N ($\times 1000$)	Density (km^{-2})	Invasions	Sims
0.1	400	5	2.5	2	0.8	0	97
0.1	400	10	5.0	4	0.8	0	100
0.1	400	20	10.0	8	0.8	2	100
0.1	400	40	20.0	16	0.8	2	100
0.1	400	80	40.0	32	0.8	7	100
0.2	400	5	2.5	2	0.8	2	99
0.2	400	10	5.0	4	0.8	1	100
0.2	400	20	10.0	8	0.8	0	100
0.2	400	40	20.0	16	0.8	3	100
0.2	400	80	40.0	32	0.8	11	100
0.3	400	5	2.5	2	0.8	1	96
0.3	400	10	5.0	4	0.8	2	100
0.3	400	20	10.0	8	0.8	7	100
0.3	400	40	20.0	16	0.8	15	100
0.3	400	80	40.0	32	0.8	17	100

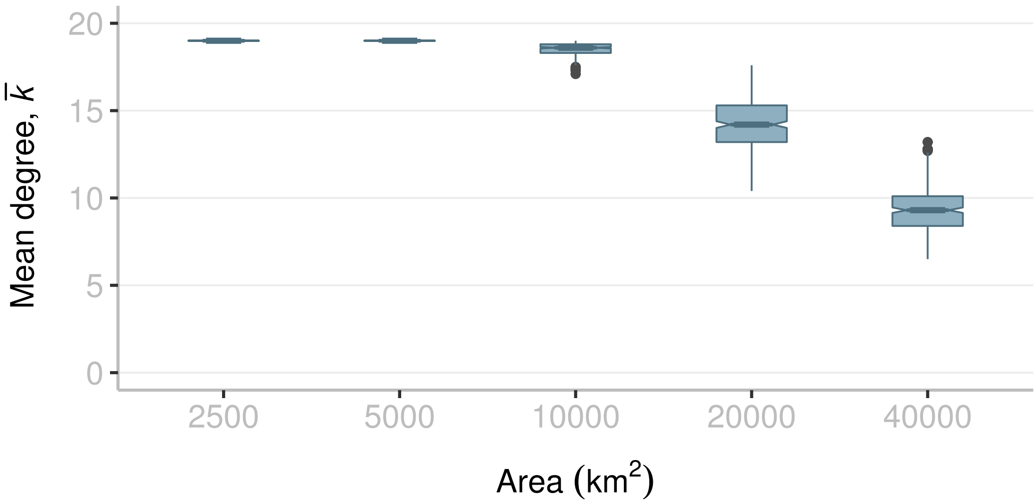

FIGURE S1. Change in average metapopulation network degree ($\bar{k}$) with increasing range size. Bars show the median, boxes show the interquartile range, vertical lines show the range and grey dots indicate outlier values. Notches indicate the 95% confidence interval of the median. All simulations had 20 colonies, meaning 19 is the maximum value of $\bar{k}$.

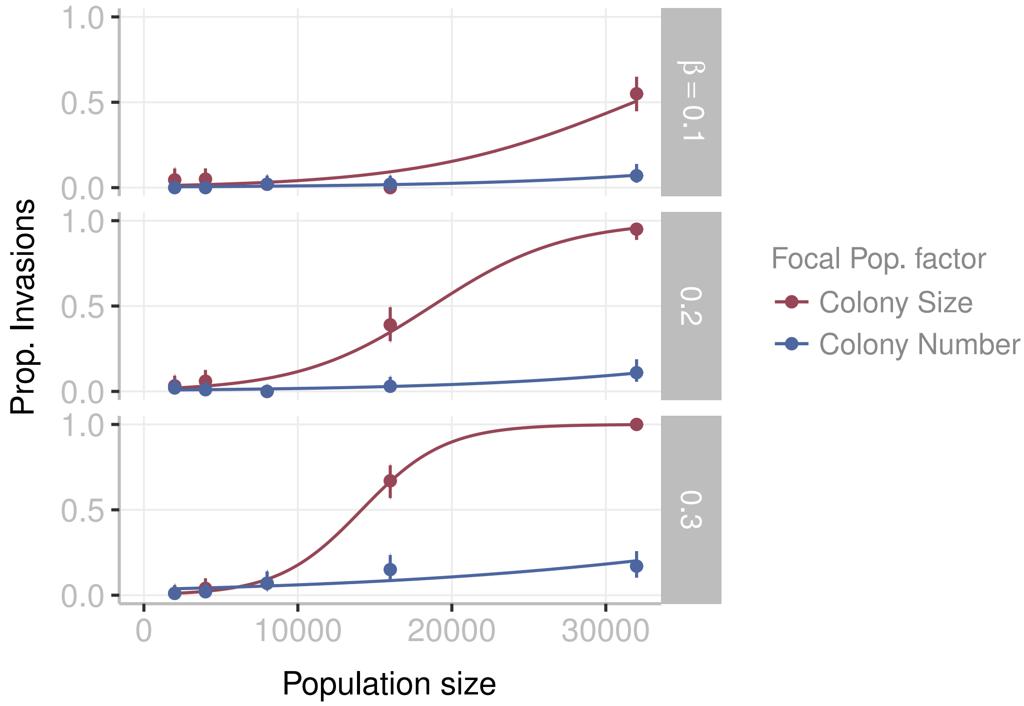

FIGURE S2. Comparison of the effect of host population size on probability of invasion when population size is altered by changing colony size or colony number. Relationships are shown separately for each transmission value, β. It can be seen that changes in colony size give a much greater increase in invasion probability than changes in colony number. Note that this is the same data as Figure 3 in the main manuscript but with the x-axis scaled by population size, rather than relative parameter change.

References

[1] R Development Core Team. *R: A language and environment for statistical computing*. R Foundation For Statistical Computing. Vienna, Austria, 2010. URL: `http://www.R-Project.org`.

[2] TCD Lucas. "MetapopEpi: Functions to run multipathogen, metapopulation epidemiological simulations" (2015). R package version 0.0.1. DOI: `10.5281/zenodo.48942`. URL: `https://github.com/timcdlucas/metapopepi`.

[3] C Castillo-Chavez, H Hethcote, V Andreasen, S Levin, and WM Liu. "Epidemiological models with age structure, proportionate mixing, and cross-immunity". *J. Math. Biol.* 27.3 (1989), pp. 233–258. DOI: `10.1007/BF00275810`.