

Appendix S1

Evolution of transmission and virulence

We here wish to investigate whether the evolutionary pressures under which the virulence and transmission of MEs will evolve can be sufficiently high to bring about the extinction of the whole population. To this end, we extend the dynamics described in the simple two-state model, in the main text, to include a mutant host strain which has a different amount of horizontal transfer β_m and ME-induced mortality μ_m that differs very slightly from that of the host (i.e. $\beta_m = \beta + \delta$ and $\mu_m = \mu + \delta$, where $\delta \rightarrow 0$). Writing the density of individuals infected by the mutant ME as n_{Im} , the overall population density then becomes $N_T = n_S + n_I + n_{Im}$. The evolutionary dynamics of the mutant strain is given by

$$dn_{Im}/dt = n_{Im}(r(1-N_T/k) + \beta_m n_S - x - \mu_m - \theta) \quad (S1)$$

Applying the quotient rule, these dynamics become:

$$dq_m/dt = q_m (\beta_m (1-q-q_m) - x + q\mu + q_m\mu_m - \mu_m) \quad (S2)$$

As we assume that the frequency of mutant MEs is negligible (i.e. that $q_m \rightarrow 0$), and that any mutant MEs will therefore have no affect on the host population density, the total population density is given by $N_T = n_S + n_I$. As our analysis is based on adaptive dynamics (Geritz et al., 1998, Metz et al., 1996, Metz et al., 1992), we assume that ecological dynamics occur on a much shorter time-scale than evolutionary dynamics, and that the population of hosts infected with the resident ME population is at equilibrium. From the main text, the equilibrium density of all individuals is

$$N^* = k(r(\beta - \mu) - \beta(\theta + \mu) + \mu(x + \theta + \mu)) / (r(\beta - \mu))$$

and the equilibrium proportion of infected cells is

$$q^* = 1 - x / (\beta - \mu).$$

The invasion fitness of the mutant (the condition under which the mutant will invade the resident population when rare) follows then from equation (S2):

$$w_m = (x(\beta - \beta_m) + (\mu - \beta)(\mu - \mu_m)) / (\mu - \beta) \quad (\text{S3})$$

We now assume that there is a trade-off between the cost of an ME and its transmission rate: the more the element is able to transmit (for example, by increased copy number within a host – Paulsson, 2002) the greater the cost to the host. Specifically, we assume that the overall cost is $\mu = v\beta$ (and thus $\mu_m = v\beta_m$ for the mutant). Substituting this expression into equation S3, the invasion fitness now becomes:

$$w_m(\beta_m, \beta) = (x - v\beta(1-v))(\beta_m - \beta) / ((1-v)\beta) \quad (\text{S4})$$

The optimal transmission rate can be calculated by solving the derivative $\partial w_m / \partial \beta_m$ for β , under the limit when $\beta_m \rightarrow \beta$. The ESS is

$$\beta^* = x / (v(1-v)).$$

Following Geritz *et al.* (1998), this ESS will be convergently stable (i.e. the population will evolve towards the ESS) if

$$2(1-\nu)v^2/x > 0,$$

which, since ν and x are always positive, will hold if $\nu < 1$. Following the condition for ME-mediated extinction given by

$$\beta > \mu - \mu x / (r - \theta - \mu)$$

and

$$\mu > r - \theta,$$

and applying the trade-off function $\mu = \nu\beta$, and the optimum transmission rate of

$$\beta^* = x / (\nu(1-\nu)),$$

the transmission rate of MEs in the population will evolve towards the extinction threshold if $\nu < 1$ and $x > r - \theta$, or, in other words, if transmission affects host mortality weakly enough, or if the net *per capita* growth rate is high enough.

Appendix S2

Analytical model of multiple mobile elements

The model in the main text assumes that the costs of bearing mobile elements (MEs) is the same, regardless of the number of elements within the genome. However, some genomes may harbour multiple copies of MEs (Sawyer et al., 1987, Wagner, 2006, Touchon & Rocha, 2007). We therefore extend the basic analytical model to incorporate a variable copy number within genomes, whilst still retaining some analytical tractability. To do this, we build a model with three types of cells, namely uninfected cells (which have a density n_0) cells which are infected with 1 element (which have a density n_1), and cells which are infected with more than one element (which have a density n_2). To make our model tractable, we assume that only genomes that have no elements can be infected by infected cells (at a rate β), but that the full number of elements (either one, if the infected cell is n_1 , or more than one, if the infected cell type is n_2) are transferred to an uninfected cell at a rate β . This transfer rate can be either density- ($s=1$) or frequency-dependent ($s=0$). Similarly, when elements are lost from a genome (at rate x) we assume that all elements are lost. We also assume that elements can duplicate within a genome at rate a , in which case n_1 cells with only one element become n_2 cells. The dynamics now become:

$$\frac{dn_0}{dt} = n_0 \left(r \left(1 - \frac{N_T}{k} \right) - \frac{\beta(n_1 + n_2)}{s + (1-s)N_T} - \theta \right) + x(n_1 + n_2) \quad (\text{S5a})$$

$$\frac{dn_1}{dt} = n_1 \left(r \left(1 - \frac{N_T}{k} \right) - \mu_1 - x - a + \frac{\beta n_0}{s + (1-s)N_T} - \theta \right) \quad (\text{S5b})$$

$$\frac{dn_2}{dt} = n_2 \left(r \left(1 - \frac{N_T}{k} \right) - \mu_2 - x + \frac{\beta n_0}{s + (1-s)N_T} - \theta \right) + a n_1 \quad (\text{S5c})$$

which, setting $s=0$ and scaling to proportions, we can rewrite as

$$\frac{dN_T}{dt} = N_T \left((r - \theta - q_1\mu_1 - q_2\mu_2) - \frac{rN_T}{k} \right) \quad (\text{S6a})$$

$$\frac{dq_1}{dt} = q_1 (\beta(1 - q_1 - q_2) - a - x - \mu_1 + q_1\mu_1 + q_2\mu_2) \quad (\text{S6b})$$

$$\frac{dq_2}{dt} = q_2 (\beta(1 - q_1 - q_2) - x - \mu_2 + q_1\mu_1 + q_2\mu_2) + aq_1 \quad (\text{S6c})$$

where q_1 is the frequency (i.e., the proportion) of cells infected with only 1 mobile element, and q_2 is the frequency of cells infected with 2 or more mobile elements. From S2a, we can see that the population will be driven extinct if

$$r - \theta < q_1\mu_1 + q_2\mu_2 \quad (\text{S7})$$

There will be a stable equilibrium consisting of cells containing both one mobile element and more than one mobile element if

$$\beta > a + x + \mu_1 \text{ and } \mu_2 > \mu_1 + a \quad (\text{S8})$$

We can calculate the equilibrium frequency of cells from equations S6b and S6c as

$$q_1^* = \frac{(\beta - a - x - \mu_1)(\mu_2 - a - \mu_1)}{(\beta - a - \mu_1)(\mu_2 - \mu_1)} \quad (\text{S9a})$$

$$q_2^* = \frac{a(\beta - a - x - \mu_1)}{(\beta - a - \mu_1)(\mu_2 - \mu_1)} \quad (\text{S9b})$$

By substituting these equilibrium frequencies into equation S6a, one can show that the mobile elements will drive the population extinct if

$$r > \theta > \frac{(\beta x + r(\beta - a - \mu_1))}{(\beta - a - \mu_1)} - a - x - \mu_1 \quad (\text{S10})$$

This shows that, greater mortality μ_1 of cells which carry only one element, and greater transformation rate a favour extinction. Interestingly, the extinction criteria only depends on the death rate of cells with only one mobile element. If $\mu_1 = \mu$ and $a = 0$, inequality (S10) becomes identical to inequality (3) in the main text. As above, greater levels of horizontal gene transfer increase extinction risk. We have analysed the model described by equations (1) for both density-dependent ($s=1$) and frequency-dependent transmission ($s=0$). Figures that summarize our observations are shown in the supplementary figures (figure S2) and demonstrate that the results of this extended model are qualitatively similar to the results described in the methods.

References

- Geritz, S. A. H., Kisdi, E., Meszner, G. & Metz, J. A. J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology* 12: 35-57.
- Metz, J. A. J., Geritz, S. A. H., Meszner, G., Jacobs, F. J. A. & van Heerwaarden, J. S. (1996) Adaptive Dynamics: A Geometrical Study of the Consequences of Nearly Faithful Reproduction. In: *Stochastic and Spatial Structures of Dynamical Systems*, (van Strien, S. J. & Verduyn Lunel, M., eds.). pp. 183-231. North-Holland, Amsterdam.
- Metz, J. A. J., Nisbet, R. M. & Geritz, S. A. H. 1992. How should we define fitness for general ecological scenarios? *Trends in Ecology & Evolution* 7: 198-202.
- Paulsson, J. 2002. Multileveled selection on plasmid replication. *Genetics* 161: 1373-1384.
- Sawyer, S. A., Dykhuizen, D. E., DuBose, R. F., Green, L., Mutangadura-Mhlanga, T., Wolczyk, D. F. & Hartl, D. L. 1987. Distribution and Abundance of Insertion Sequences among natural isolates of *Escherichia coli*. *Genetics* 115: 51-63.
- Touchon, M. & Rocha, E. P. C. 2007. Causes of insertion sequences abundance in prokaryotic genomes. *Molecular Biology and Evolution* 24: 969-981.
- Wagner, A. 2006. Periodic extinctions of transposable elements in bacterial lineages: evidence from intragenomic variation in multiple genomes. *Molecular Biology and Evolution* 23: 723-733.

Figures

Figure S1. The effect of horizontal gene transfer β and the cost of mobile element infection μ on the equilibrium density of the host population (Figures S1a and S1c) and the equilibrium density of MEs in the population (Figures S1b and S1d) for the simple two-state analytical model. Results in Figures S1a and S1b are under frequency-dependent transmission (i.e. $s=0$) and Figure S1c and S1d are under density-dependent transmission (i.e. $s=1$). Parameters used in the model are $r=1$, $\theta=0.25$, $x=0.05$, $k=1000$.

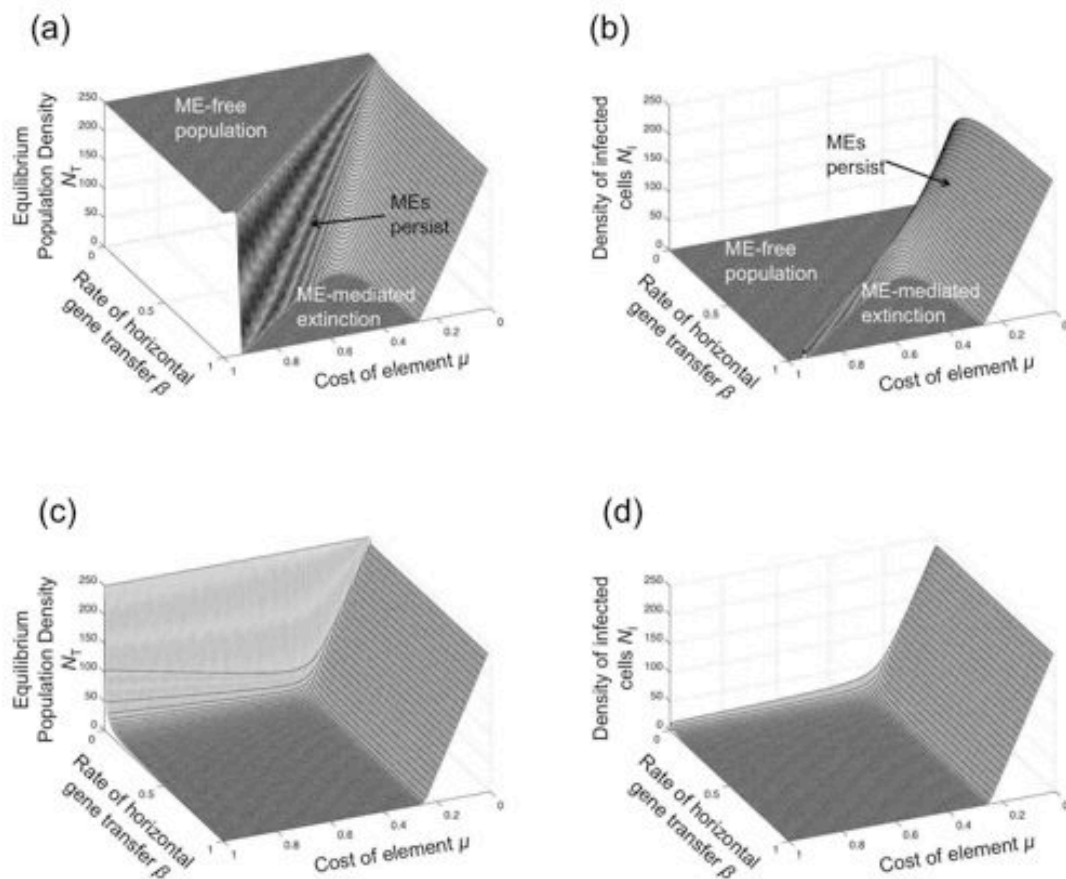


Figure S2. The effect of horizontal gene transfer β and the cost of an additional ME μ on the equilibrium density of the host population (Figures S2a and S2c) and the equilibrium density of MEs in the population (Figures S2b and S2d) for the analytical three-state model described in section 2 of the model and results the main text. Results in Figures S2a and S2b assume frequency-dependent transmission (i.e. $s=0$) and Figures S2c and S2d assume density-dependent transmission (i.e. $s=1$). Parameters used are $r=1$, $\theta=0.75$, $k=1000$, $a=0.1$, $x=0.05$.

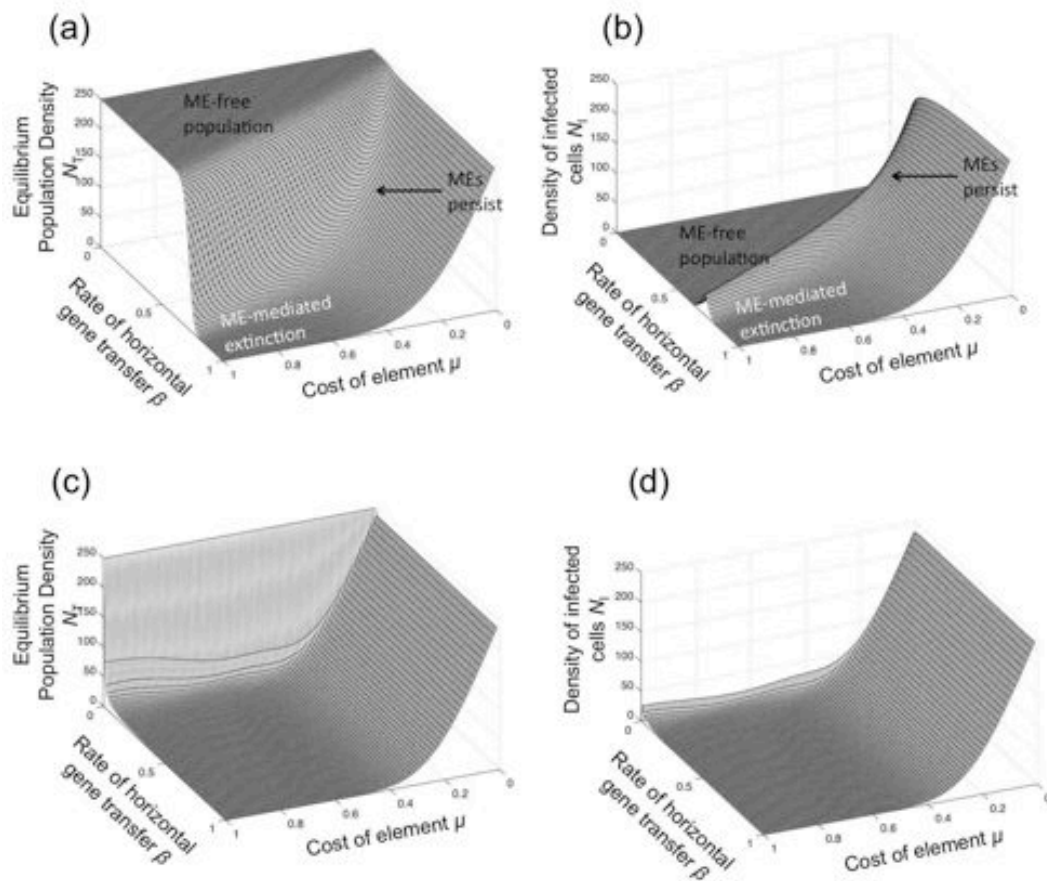


Figure S3. Diagram showing the transition dynamics for the multi-state numerical model. Parameters are described in the main text and table 1. The function $f(N_I, N_T)$ describes the mode of horizontal transfer. In our case, the per-capita rate of being infected with an additional mobile element is $f(N_I, N_T)\beta = \beta N_I(s + (1-s)/N_T)$ where s determines the mode of transmission (density-dependent or frequency-dependent).

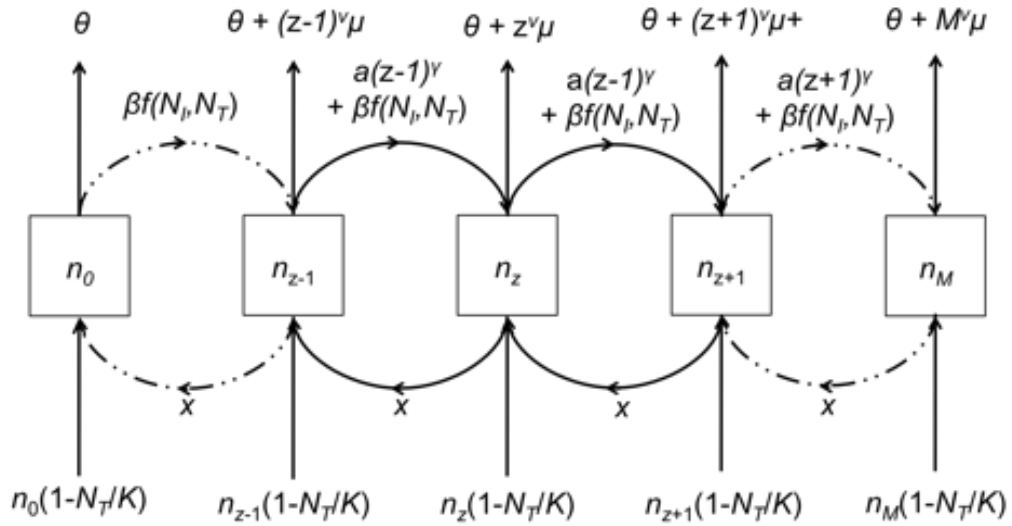


Figure S4. The effect of horizontal gene transfer β and the cost of an additional ME μ on the equilibrium density of the host population (Figures S4a and S4c) and the equilibrium density of MEs in the population (Figures S4b and S4d) for the numerical model described in figure S3. Results in Figures S4a and S4b are under frequency-dependent transmission (i.e. $s=0$) and Figures S4c and S4d are under density-dependent transmission (i.e. $s=1$). Parameters used are $r=1$, $\theta=0.75$, $k=1000$, $a=0.1$, $M=500$, $\nu=2$, $x=0.05$, $\gamma=0$.

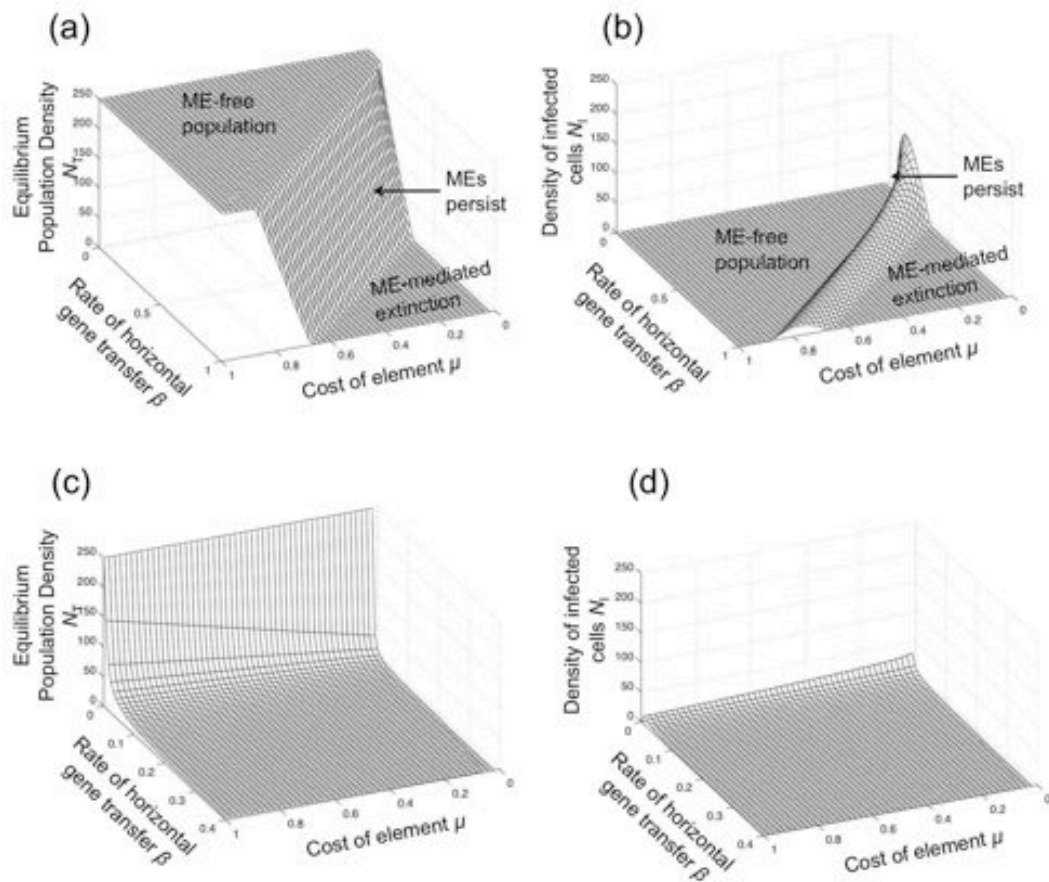


Figure S5. The effect of horizontal gene transfer β and the cost of an additional ME μ on the equilibrium density of the host population (Figures S5a and S5c) and the equilibrium density of MEs in the population (Figures S5b and S5d) for the numerical model described in figure S3. Results in Figures S5a and S5b are under frequency-dependent transmission (i.e. $s=0$) and Figures S5c and S5d are under density-dependent transmission (i.e. $s=1$). Parameters used are $r=1$, $\theta=0.75$, $k=1000$, $a=0.1$, $M=500$, $\nu=1/2$, $x=0.05$, $\gamma=0$.

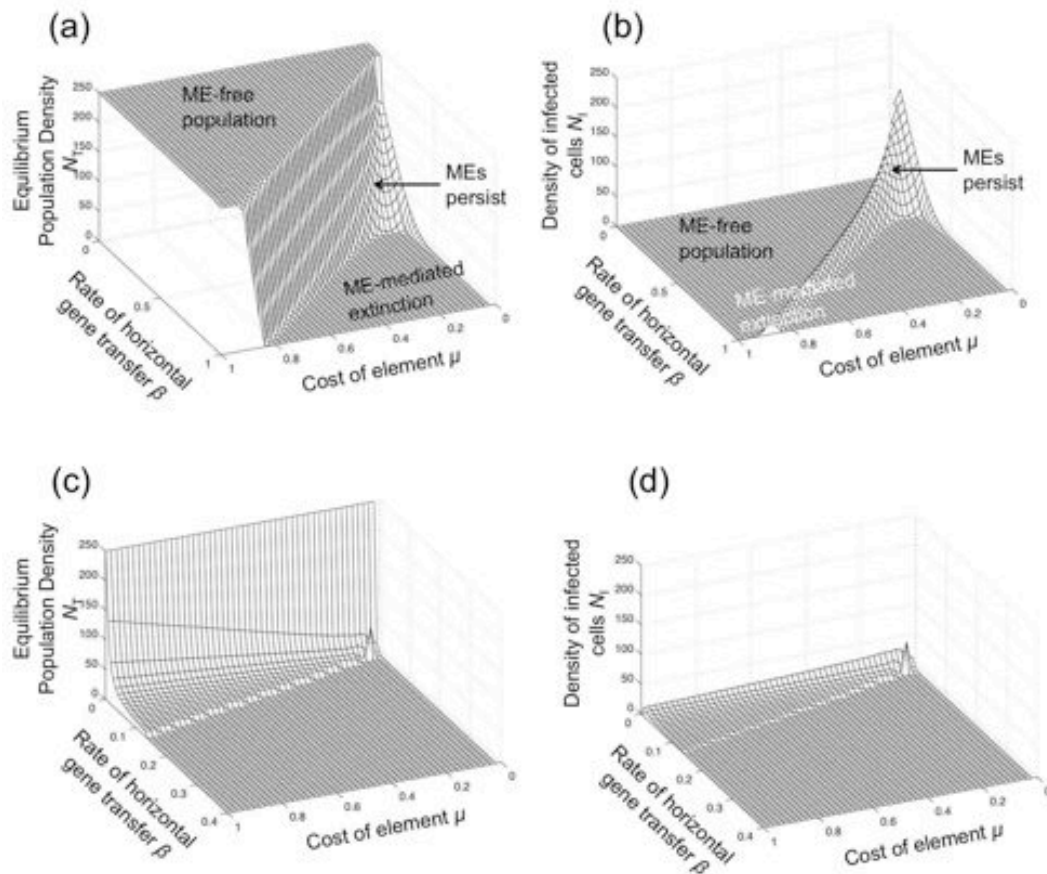


Figure S6 The effect of horizontal gene transfer β and the cost of an additional ME μ on the equilibrium density of the host population (Figures S6a and S6c) and the equilibrium density of MEs in the population (Figures S6b and S6d) for the numerical model. Results in Figures S6a and S6b are for frequency-dependent transmission (i.e. $s=0$), and results in Figures S6c and S6d are for density-dependent transmission (i.e. $s=1$). Parameters used are $r=1$, $\theta=0.75$, $k=1000$, $a=0.1$, $M=500$, $v=1$, $x=0.05$, $\gamma=0$.

