



Diffusion versus dispersal wave-of-advance models and Neolithic spread

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1. reaction-diffusion vs reaction-dispersal

Fisher's equation

$$\frac{\partial F}{\partial t} = D_F \nabla^2 F + a_F F \left(1 - \frac{F}{K_F} \right)$$

$F = F(x, y, t)$ = population density (e.g., farmers)

D_F = diffusion coefficient

Logistic growth:

a_F = initial growth rate

K_F = carrying capacity

speed of range expansions = $2\sqrt{a_F D_F}$

Fisher's equation is only an approximation*, obtained from:

$$\begin{aligned} F(x, y, t + T) - F(x, y, t) &= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} F(x + \Delta_x, y + \Delta_y, t) \phi_F(\Delta_x, \Delta_y) d\Delta_x d\Delta_y \\ &\quad - F(x, y, t) + R_T[F(x, y, t)] - F(x, y, t) \end{aligned}$$

↙ Logistic

*Fort & Méndez, Phys. Rev. Lett. (1999)

We will compare the speed from this equation to Fisher's approximation = $2\sqrt{a_F D_F}$

Preindustrial populations (farmers)

- Population A*: $\{p_j\}=\{0.54, 0.17, 0.04, 0.25\}$,
 $\{r_j\}=\{2.4, 14.5, 36.3, 60.4\}$ km.
- Population B*: $\{p_j\}=\{0.40, 0.17, 0.17, 0.26\}$,
 $\{r_j\}=\{2.4, 14.5, 36.3, 60.4\}$ km.
- Population C*: $\{p_j\}=\{0.19, 0.07, 0.22, 0.52\}$,
 $\{r_j\}=\{2.4, 14.5, 36.2, 60.4\}$ km.
- Population D**: $\{p_j\}=\{0.19, 0.54, 0.17, 0.04, 0.04, 0.02\}$,
 $\{r_j\}=\{5, 30, 50, 70, 90, 110\}$ km.
- Population E***: $\{p_j\}=\{0.42; 0.23; 0.16; 0.08; 0.07; 0.02; 0.01; 0.01\}$,
 $\{r_j\}=\{2.3, 7.3, 15, 25, 35, 45, 55, 100\}$ km.

*Ethiopia; **Brazil; ***Central African Republic

Preindustrial populations (farmers)

Values of a_F and T :

$0.023 \text{ y}^{-1} \leq a_F \leq 0.033 \text{ y}^{-1}$ (from 4 ethnographic and 1 archaeological populations)

$T = 32 \text{ y}$ (from ethnographic data)

Population	speed (km/yr)	Fisher (km/yr)	error Fisher
A	0.71-0.81	0.85-1.02	20%-26%
B	0.75-0.84	0.93-1.11	24%-32%
C	0.92-1.01	1.26-1.51	37%- <u>50%</u>
D	0.93-1.06	1.11-1.34	19%-26%
E	0.61-0.74	0.54-0.65	-11%--12%

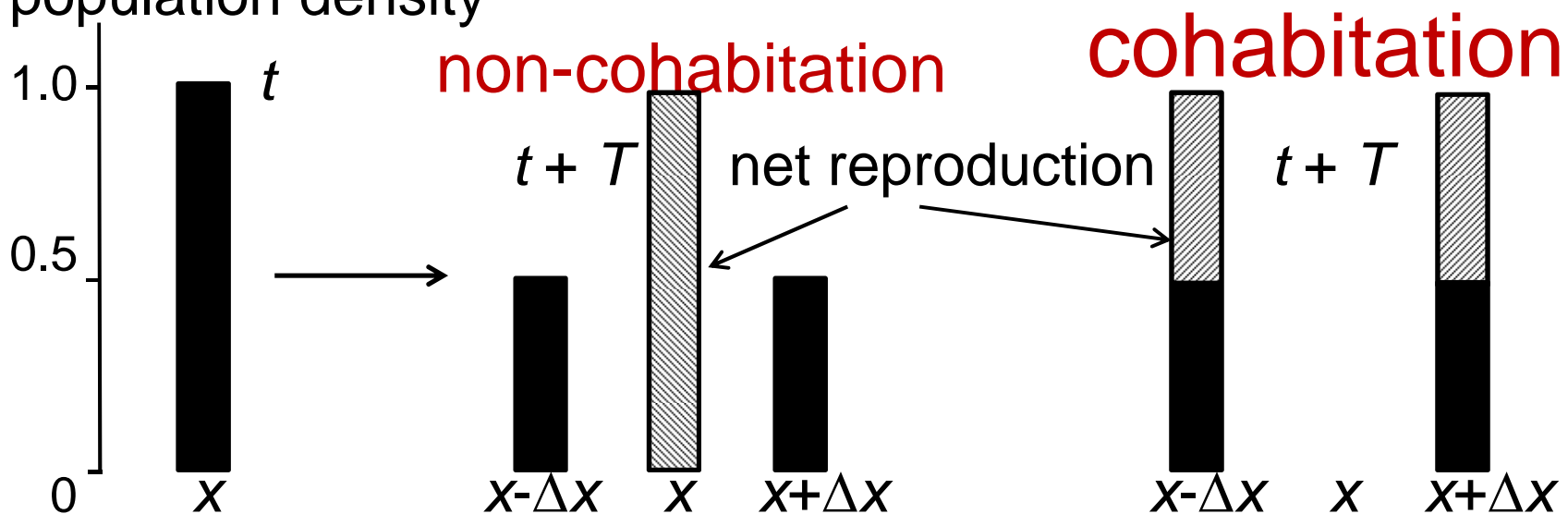
2. non-cohabitation vs cohabitation eqs.

Up to now: non-cohabitation eq.: $F(x, y, t + T) - F(x, y, t) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} F(x + \Delta_x, y + \Delta_y, t) \phi_F(\Delta_x, \Delta_y) d\Delta_x d\Delta_y - F(x, y, t) + R_T[F(x, y, t)] - F(x, y, t)$

Cohabitation equation:

$$F(x, y, t + T) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} R_T[F(x + \Delta_x, y + \Delta_y, t)] \phi_F(\Delta_x, \Delta_y) d\Delta_x d\Delta_y$$

population density



Preindustrial populations (farmers)

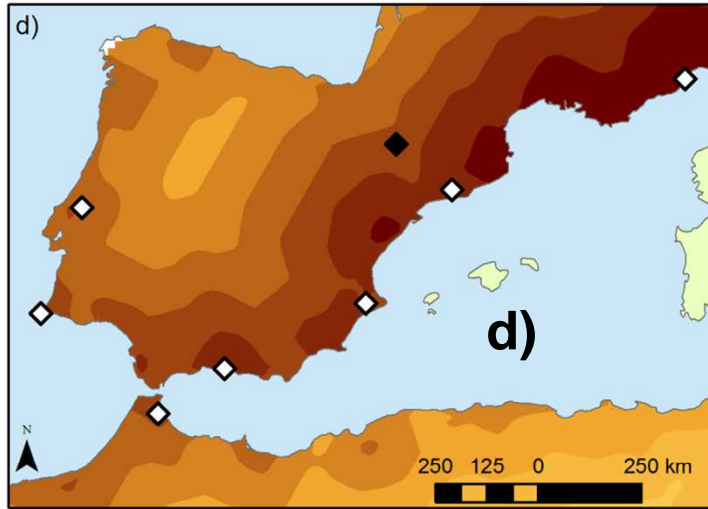
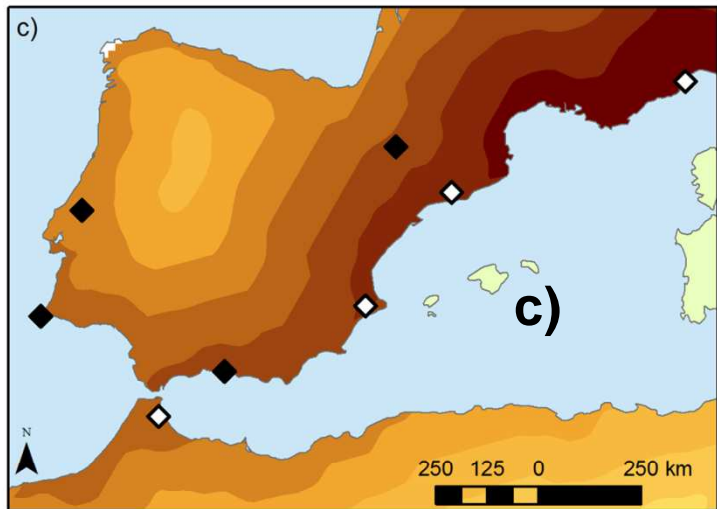
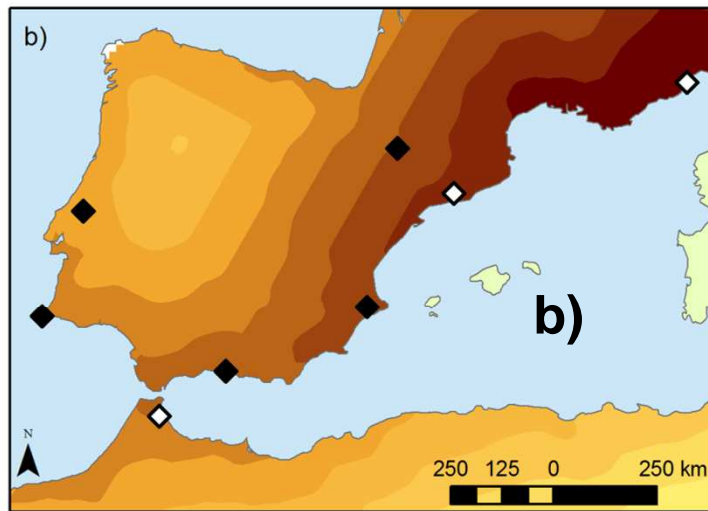
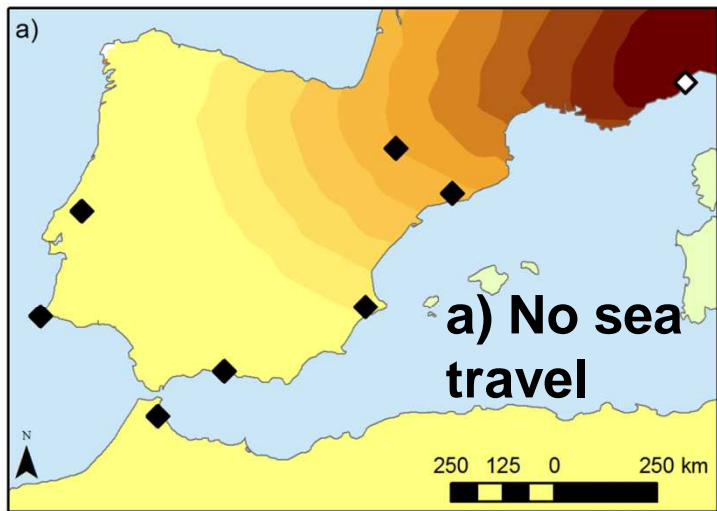
Population	Cohabitation (km/yr)	error non-cohab. (relative to cohab.)	error Fisher (relative to cohab.)
A	0.91-1.10	-22%--26%	-6%--8%
B	0.96-1.15	-22%--27%	-5%--3%
C	1.20-1.40	-23%-- <u>28%</u>	5%-8%
D	1.18-1.44	-21%--26%	-6%--7%
E	0.74-0.94	-18%--22%	27- <u>31%</u>

Another way to see the limitations of Fishers' eq.:

$$\text{Fisher's speed} = 2\sqrt{a_F D_F} \rightarrow \infty \text{ if } a_F \rightarrow \infty$$

$$\text{Cohabitation speed}^* \rightarrow \frac{r_{max}}{T} \text{ if } a_F \rightarrow \infty$$

$$* \text{ cohabitation speed} = \min_{\lambda > 0} \frac{a_F T + \ln \left[\sum_{j=1}^M p_j I_0(\lambda r_j) \right]}{T \lambda}$$



b)-d) Sea travel up to 350 km

b) preference for closer destinations

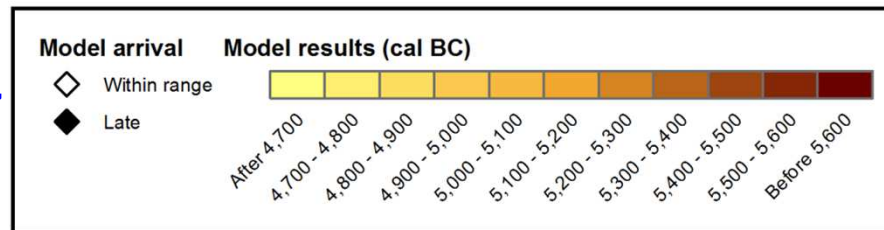
b) all distances within 350 km equally likely

b) all jumps of 350 km

◇ within range

◆ too late

Isern, Zilhao, Fort & Ammerman, PNAS 2017



3. With cultural transmission ($F = \text{farmers}$, $H = \text{HGs}$)

$$\begin{cases} F(x, y, t + T) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \tilde{F}(x + \Delta_x, y + \Delta_y, t) \phi_F(\Delta_x, \Delta_y) d\Delta_x d\Delta_y \\ H(x, y, t + T) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \tilde{H}(x + \Delta_x, y + \Delta_y, t) \phi_H(\Delta_x, \Delta_y) d\Delta_x d\Delta_y \end{cases}$$

$$\tilde{F}(x, y, t) \equiv R_T[F(x, y, t)] + f \frac{R_T[F(x, y, t)]R_T[H(x, y, t)]}{R_T[F(x, y, t)] + \gamma R_T[H(x, y, t)]}$$

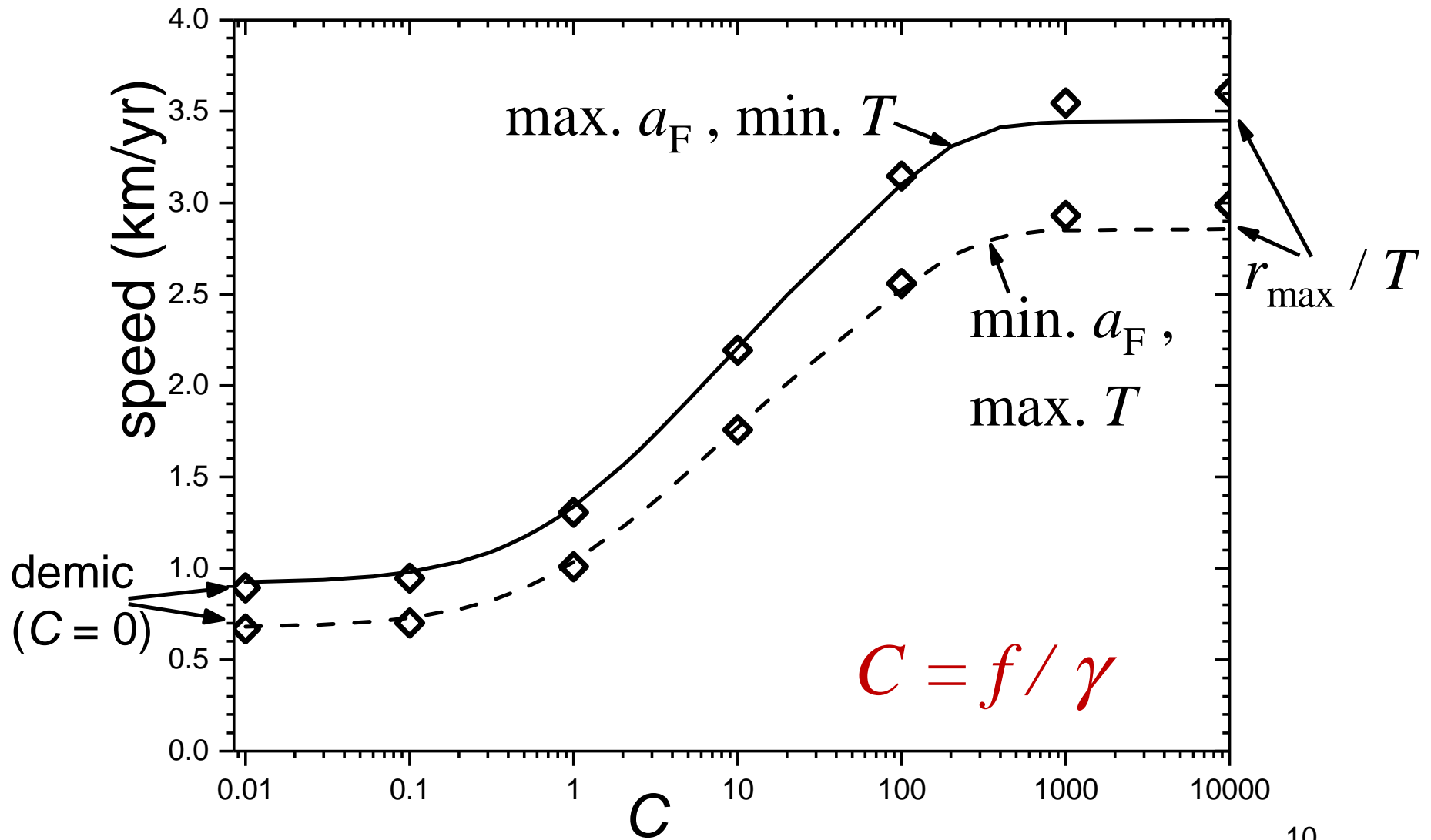
$$\tilde{H}(x, y, t) \equiv R_T[H(x, y, t)] - f \frac{R_T[F(x, y, t)]R_T[H(x, y, t)]}{R_T[F(x, y, t)] + \gamma R_T[H(x, y, t)]}$$

$$R_T[F(x, y, t)] = \frac{e^{a_F T} K_F F(x, y, t)}{K_F + (e^{a_F T} - 1) F(x, y, t)}$$

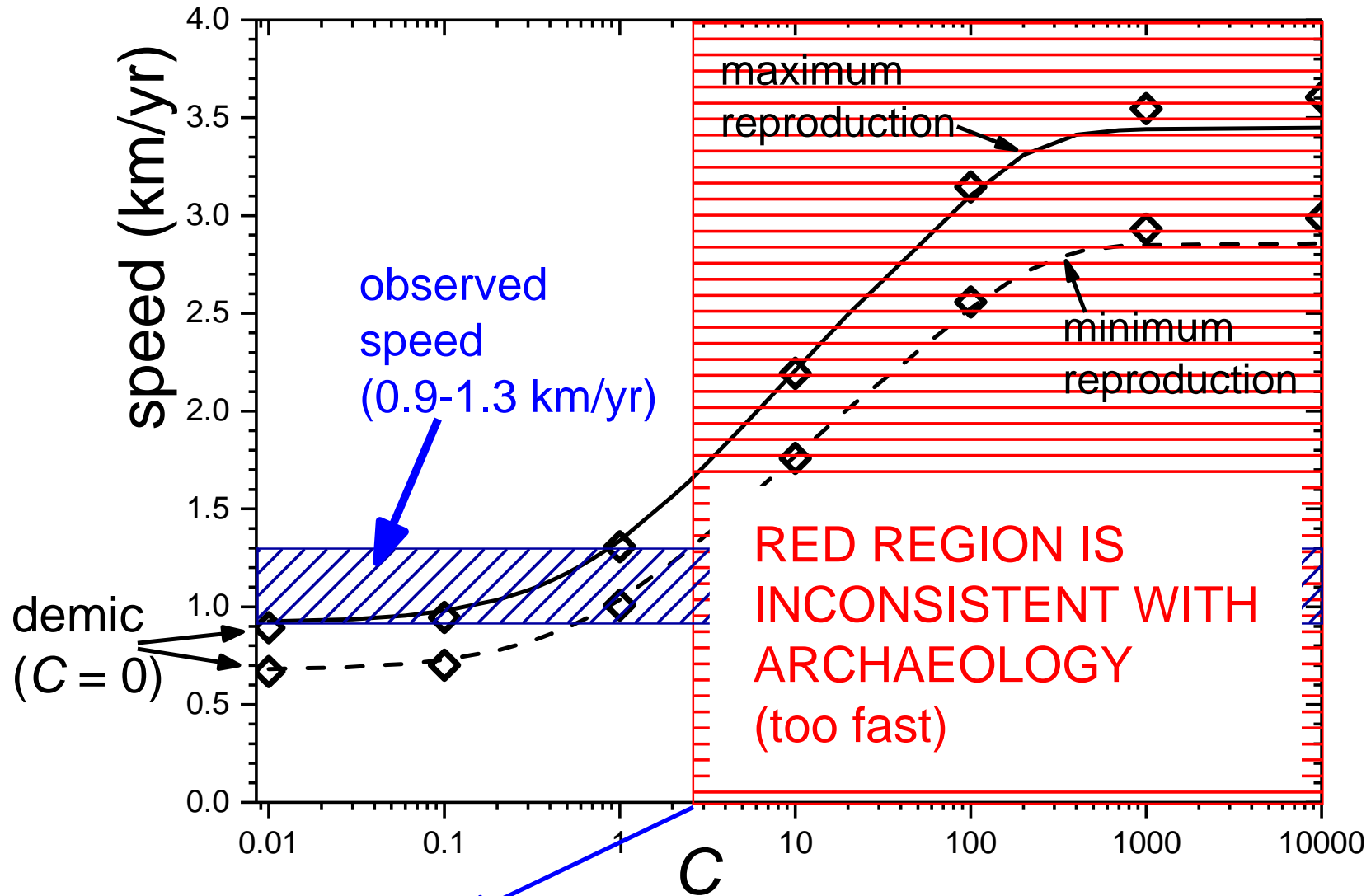
$$R_T[H(x, y, t)] = \frac{e^{a_H T} K_H H(x, y, t)}{K_H + (e^{a_H T} - 1) H(x, y, t)}$$

Plot of the front speed using the Eqs. in the previous slide

◇ simulations =- equation



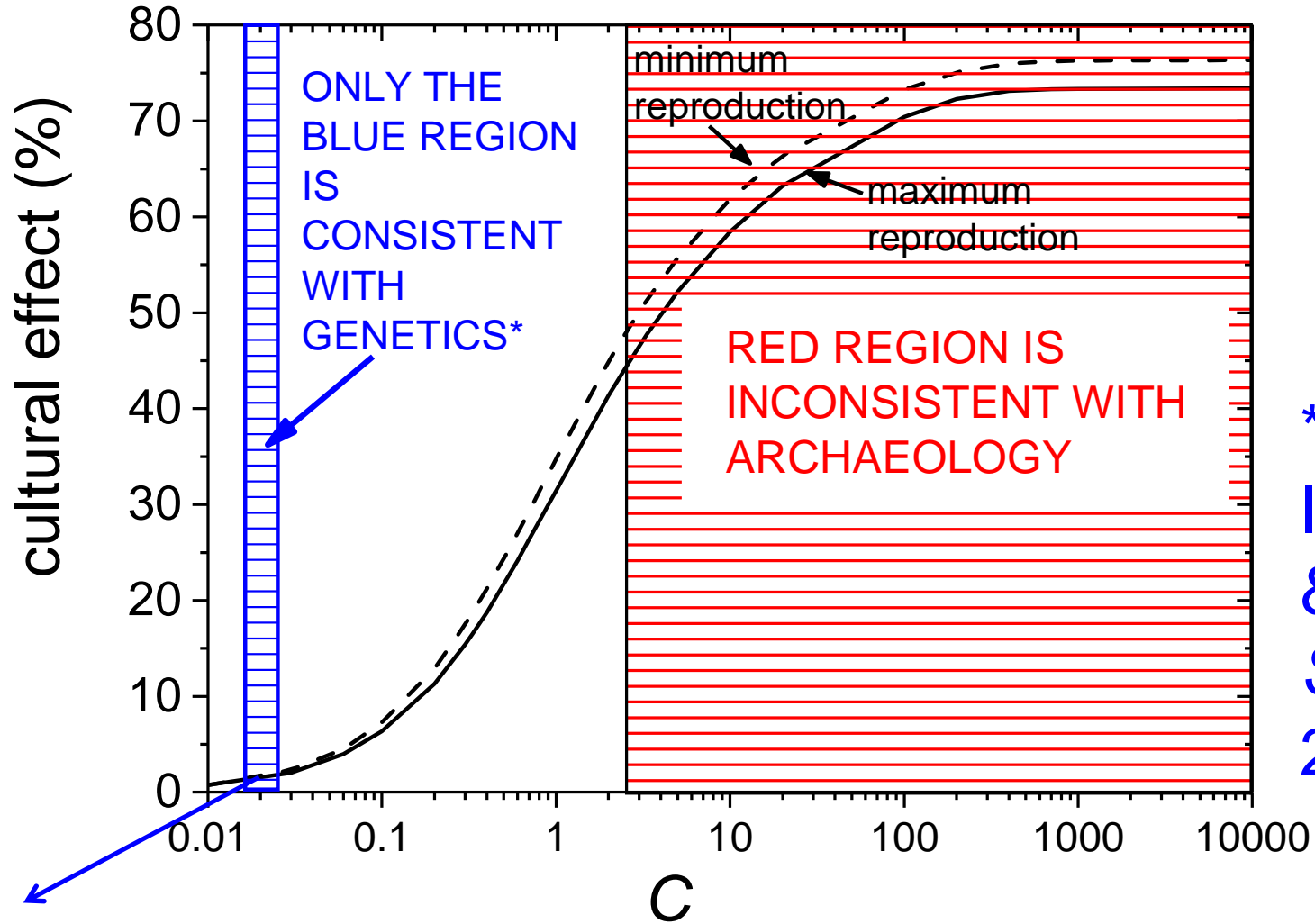
— equations ◇ simulations



$C < 3$, so less than 3 HGs were converted per F per generation

Fort, *PNAS* (2012)

$$\text{Effect (\%)} = (\text{speed} - \text{demic speed}) / \text{speed} \cdot 100$$



*Genetics:
Isern, Fort
& Rioja,
Sci. Rep.
2017

cultural effect of only 2%, so demic >> cultural