File S1

The impact of dominance on adaptation in changing environments

Supporting Information

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S1 Discrete and continuous time models for diploids

Consider a randomly mating population of N diploids with discrete generations in which the selection acts on the viability of an individual. Then the life cycle consists of a juvenile phase during which mutation, selection and random genetic drift act, and determine the chance of survival of an individual to the adult phase in which reproduction occurs. For a large population, immediately after random mating, the frequency of the genotypes can be approximated by the corresponding Hardy-Weinberg proportions as the deviations from it are of order $1/N$ (Nagylaki, 1992). The dynamics in the juvenile phase can be modeled by a discrete time Wright-Fisher process (Ewens, 2004).

In contrast to the discrete time model described above, in the main text, we worked with a continuous time model as the environment is assumed to change gradually. In overlapping generations, a model that incorporates details of the life cycle is necessarily complex as the age-structure of the population must be carefully taken into account. Moreover, besides large N, additional assumptions, viz., small selection coefficient, s and mutation probability, μ are required for Hardy-Weinberg equilibrium to hold in such continuous time models (Nagylaki, 1992).

However, in the diffusion approximation where $s \to 0, \mu \to 0, N \to \infty$ with finite $2Ns, 2N\mu$ in the continuous time model and $4Ns, 4N\mu$ in the discrete time model, we obtain essentially the same Kolmogorov equations for both models (Ewens, 2004). In the main text, we studied the dynamics of adaptation in the framework of diffusion theory when the mutant is on average neutral as the $\bar{s} \neq 0$ case does not seem to be analytically tractable.

However, for positive $\bar{s}$, it is possible to make analytical progress by modeling the fixation process as a branching process (Desai and Fisher, 2007; Uecker and Hermisson, 2011). The branching approximation applies as long as the mutants are rare, that is, a finite number of mutants are present in an infinitely large population. In this approximation, the transition rate matrix for the discrete time model discussed above is not a continuant matrix (Ewens, 2004). However, as the number of mutants is small, it is reasonable to assume that the transition rates are significantly different from zero only when the number of mutant allele changes by one in a generation; in other words, we arrive at a birth-death model. The above discussion thus provides a justification for the birth-death model for diploids and in the main text, we have used it for all parameter regimes.

S2 Fixation probability of a mutant that is beneficial at all times

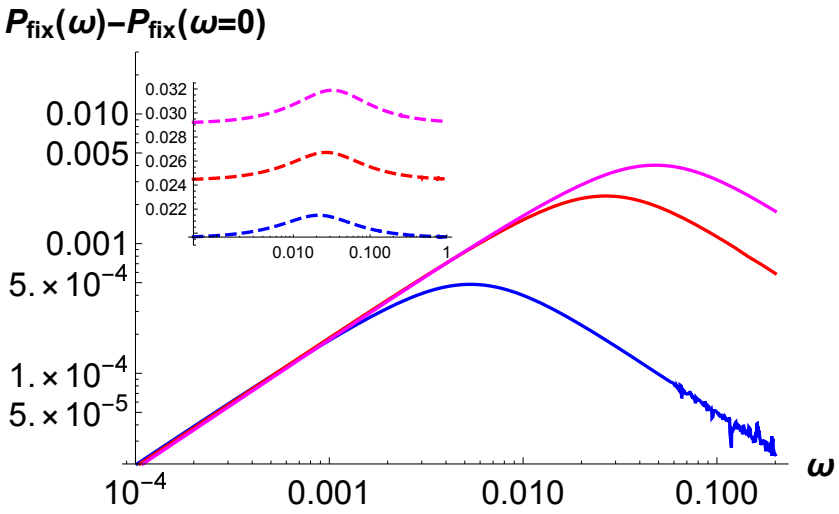

Figure S1: The inset shows the fixation probability $P_{\text{fix}}(\omega)$ given by (5) for a mutant that is beneficial on average for dominance coefficient $h = 0.4, 0.5, 0.6$ (bottom to top). In the main figure, the effect of a changing environment is shown by subtracting the fixation probability $P_{\text{fix}}(\omega = 0) = hs(t_a)/[1 + hs(t_a)]$ with $s(t_a) = \bar{s} + \sigma \sin(\theta_a)$ for $h = 0.1, 0.5, 0.9$ (bottom to top). In both plots, $\bar{s} = 0.05, \sigma = 0.2\bar{s}, \theta_a = 0$.

S3 Fixation probability of an on average neutral mutant

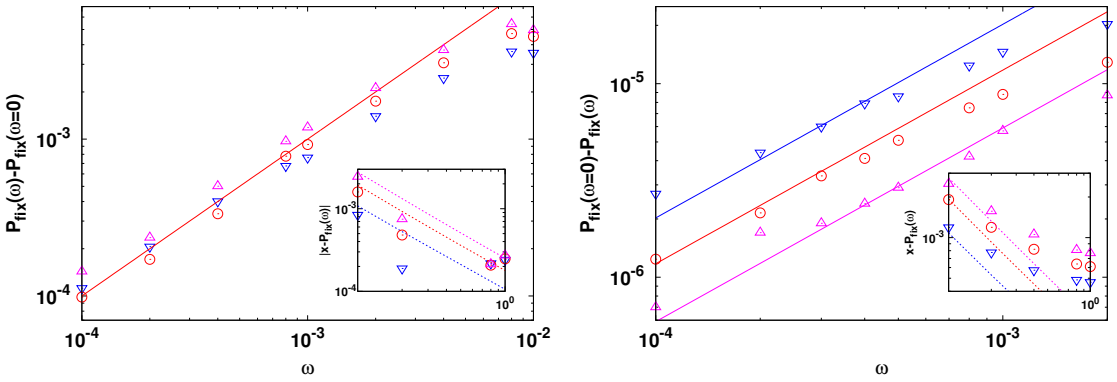

Figure S2: Fixation probability of a mutant that is neutral on average for $N\sigma \gg 1$ when the mutant appeared at $\theta_a = \pi/4$ (left panel) and $5\pi/4$ (right panel). The solid line shows the expression (11b) (left panel) and (11c) (right panel) for small cycling frequencies and the dashed lines represent (8b) for large cycling frequencies. Here $N = 100, \sigma = 0.1$ and $h = 0.3(\triangledown), 0.5(\circ), 0.7(\triangle)$. The numerically obtained value $P_{\rm fix}(\omega = 0) = 2.53 \times 10^{-2}, 3.40 \times 10^{-2}, 4.38 \times 10^{-2}$ for $h = 0.3, 0.5, 0.7$, respectively, for the left panel. For the right panel, $P_{\rm fix}(\omega = 0) = 3.55 \times 10^{-5}, 2.58 \times 10^{-5}, 1.98 \times 10^{-5}$ for $h = 0.3, 0.5, 0.7$, respectively. The simulation results are averaged over 10^7 runs.

S4 Fixation probability of a mutant in transiently varying selection

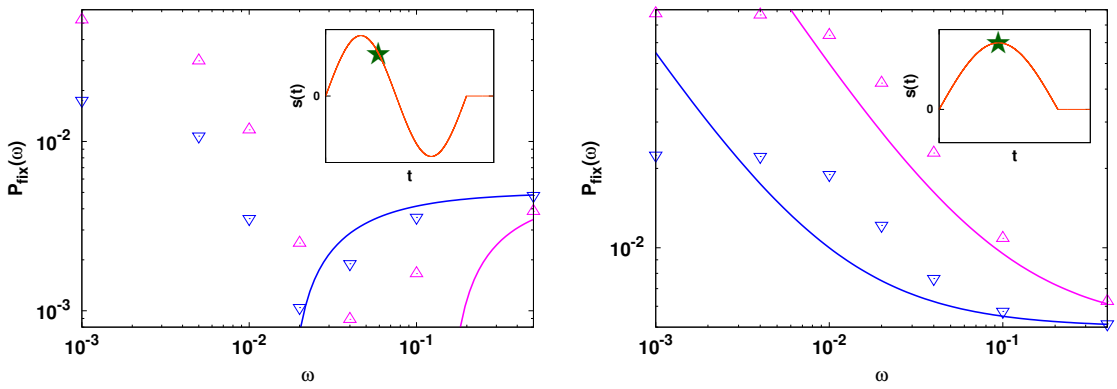

Figure S3: Fixation probability of a mutant in transiently varying environments defined by (1) and (2) and illustrated in the inset. The lines show the expression (4) and the points show the simulation data obtained by averaging over 10^7 independent runs for $\theta_a = 3\pi/4, T_e = 2\pi/\omega$ (left panel) and $\theta_a = \pi/2, T_e = \pi/\omega$ (right panel). In all the plots, $N = 100$, $\sigma = 0.1$ and $h = 0.1(\triangledown), 0.9(\triangle)$.

Here we consider a situation in which the time-averaged selection coefficient is nonzero and changes over a finite time T_e,

$$s(t) = \begin{cases} \sigma \sin(\omega t) & , \ t < T_e \qquad (1) \\ 0 & , \ t > T_e \ . \qquad (2) \end{cases}$$

Waxman (2011) has shown that in such a case, the fixation probability is simply given by the mean allele frequency at the end of selection. Here we

estimate this allele frequency using the deterministic evolution equation,

$$\dot{x} = s(t)x(1-x)(x+h(1-2x)) \overset{x\to 0}{\approx} hs(t)x \ . \tag{3}$$

For large ω, starting from a single mutant, the number of mutants at time T_e is then given by

$$2Nx(T_e) = n(T_e) = 1 + \frac{h\sigma}{\omega}\left(\cos(\theta_a) - \cos(\omega T_e)\right) \ . \tag{4}$$

For large cycling frequencies, this prediction matches qualitatively with the numerical results in Fig. S3, and therefore captures the effect of dominance when the environment changes fast over a short interval of time.

References

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Ewens, W., 2004 *Mathematical Population Genetics*. Springer, Berlin.

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