

Supplementary Information for S.Gavrilets “Human origins and the transition from promiscuity to pair-bonding”

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Effects of α and β

Figure S1 shows the effects of parameter α on female fertility $B(p)$. Figure S2 shows the expected mating success $E\{S\}$ for males of different ranks assuming maximum mating effort (i.e. all $m_i = 1$) with $N = 8$ and different values of σ and β . These graphs were obtained by generating individuals strengths s_1, \dots, s_8 by random independent sampling from a uniform distribution on $1/2 \mp \sigma/2$ and then evaluating mating success as predicted by the Tullock function

$$S_i = \frac{s_i^\beta}{\sum_j s_j^\beta}. \quad (1)$$

To produce the graphs, I used 500 randomly generated sets of data for each parameter combination. Empirical rank-mating success curves for primates typically show strong inequality in reproductive success with most of the mating going to a couple of the top-ranked males(1, 2, 3, 4). This suggests that both β and σ should be at the upper half of values considered here.

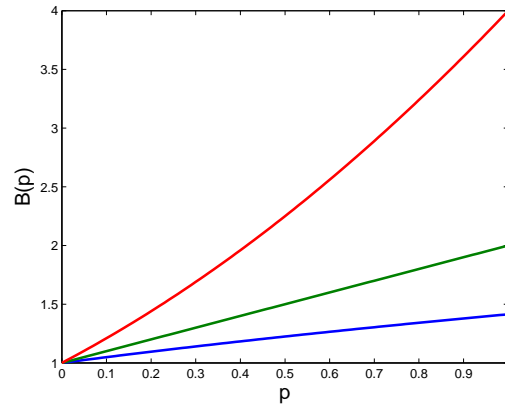
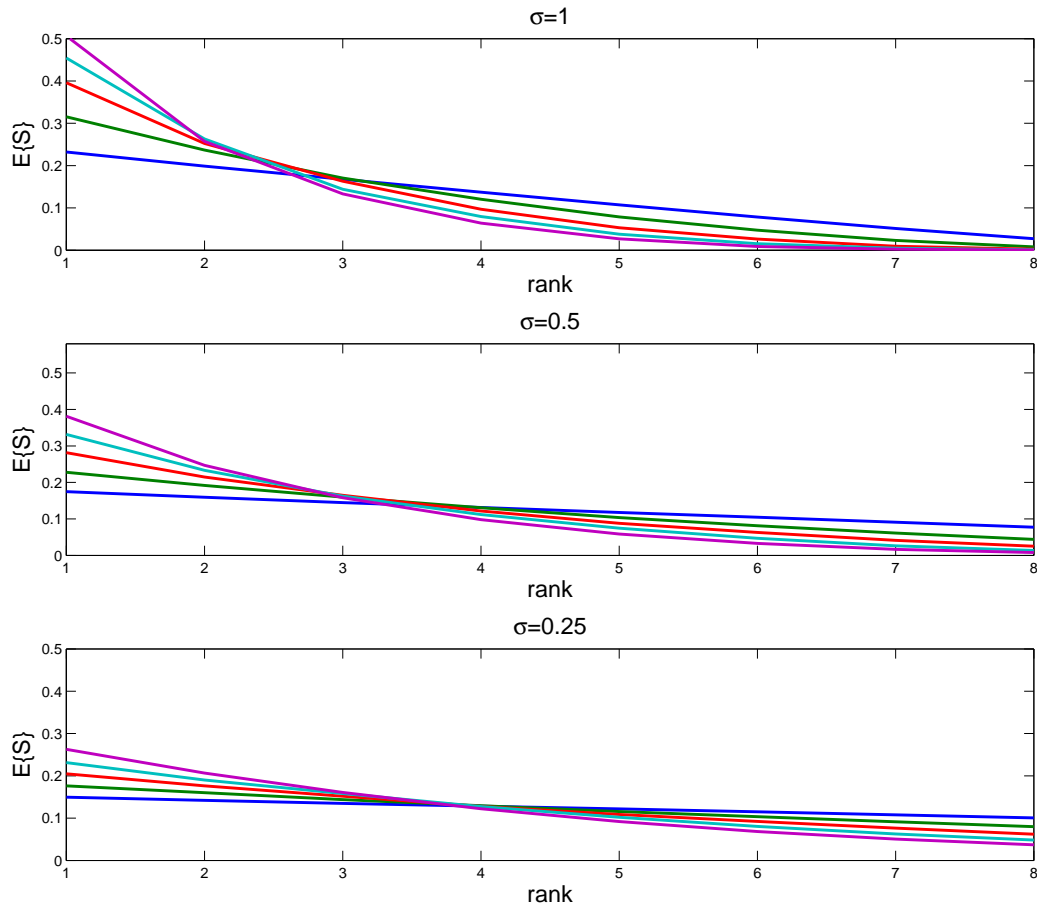


Figure S1: Female fertility $B(p) = (1+p)^\alpha$ as a function of male provisioning effort p for $\alpha = 0.5, 1$ and 2 (bottom to top).



(a)

Figure S2: Expected mating success $E\{S\}$ for males of different ranks with $N = 8$, three different values of σ (shown on the graphs), and five different values of β (1, 2, 3, 4, 5, identified by lines of different colors; bottom to top).

Communal breeding

I start by describing a model introduced by Ref.(5) and then generalizing it for the case of relatedness. Each male divides his effort between caring for offspring (c) and contending with other males for mating opportunities (m) ($c + m = 1$). Male care is distributed randomly among all offspring in the group. In a group of N male and N females, male i fitness is defined as

$$w_i = B(\bar{c})S_iN, \quad (2)$$

where \bar{c} is the average care received by offspring of a female. Using the invasion analysis, let c and m be the corresponding efforts of $N - 1$ resident males and \tilde{c} and \tilde{m} be that of a single mutant male. The invasion

fitness is

$$w(\tilde{c}|c) = B \left(\frac{\tilde{c} + (N-1)c}{N} \right) \frac{\tilde{m}^\beta}{\tilde{m}^\beta + (N-1)m^\beta} N.$$

Making substitutions $m = 1 - c$ and $\tilde{m} = 1 - \tilde{c}$ and evaluating the derivative $\frac{dw}{d\tilde{c}}$ at $\tilde{c} = c$, we find that the invasion fitness gradient is

$$\frac{dw}{dc} = \frac{(1+c)^{\alpha-1}}{N(1-c)} [-(\alpha + \beta(N-1))c - \beta(N-1) + \alpha]$$

If

$$\beta(N-1) > \alpha, \quad (3a)$$

then the expression in the brackets is always negative and c is predicted to evolve to 0. Otherwise, c evolves to an intermediate value

$$c^* = 1 - \frac{2\beta(N-1)}{\beta(N-1) + \alpha}. \quad (3b)$$

Computing the second derivative of the invasion fitness at $c = c^*$, we find that

$$\frac{d^2w}{d\tilde{c}^2} \Big|_{\tilde{c}=c} = -\frac{1}{4} \left(\frac{2\alpha}{\alpha + \beta(N-1)} \right)^\alpha \frac{(\alpha + \beta(N-1))^2}{\alpha\beta N^2(N-1)} [\beta(N-1) + \alpha(N + \beta)]$$

which is always negative. Therefore, the equilibrium c^* is evolutionarily stable.

Relatedness. The above analysis can be extended to the case when males in the group are related. Specifically I assume that on average there is not one but k mutants in a group and write k as $k = 1 + r(N-1)$. Here r is the probability that a random group-mate of a mutant is also mutant. Within the framework of our invasion analysis when mutants are rare, r is the average relatedness coefficient in the group (6). In general, r will depend on some model details which however is irrelevant for our derivations. What is necessary though is that r remains approximately constant during evolutionary dynamics. With equal individuals contributing equally on average to the next generation offspring and with small changes in c and m per generation, the assumption of approximate constancy of r is justified. Then the invasion fitness becomes

$$w(\tilde{c}|c) = B \left(\frac{k\tilde{c} + (N-k)c}{N} \right) \frac{\tilde{m}^\beta}{k\tilde{m}^\beta + (N-k)m^\beta} N.$$

while the equations (3a) and (3b) become

$$\beta(N-1) \frac{1-r}{1+r(N-1)} > \alpha,$$

$$c^* = 1 - \frac{2\beta(N-1)(1-r)}{\beta(N-1)(1-r) + \alpha[1+r(N-1)]},$$

respectively. These equations have a bit more compact form if one uses k instead of r .

Mate guarding

In this model, each male divides his effort between guarding a particular female (g) and contending with other males for mating opportunities (m) ($g + m = 1$). Assume first that guarding is 100% efficient. Male i fitness is

$$w_i = g_i + S_i \sum_j (1 - g_j), \quad (4)$$

where the sum describes the total share of paternity open for competition. Using the same notation as above, the invasion fitness can be written as

$$w(\tilde{g}|g) = \tilde{g} + \frac{\tilde{m}^\beta}{\tilde{m}^\beta + (N-1)m^\beta} [1 - \tilde{g} + (N-1)(1-g)],$$

where $m = 1 - g$, $\tilde{m} = 1 - \tilde{g}$. The invasion fitness gradient is

$$\frac{dw}{dg} = \frac{N-1}{N} (1 - \beta),$$

so that g evolves to 0 if

$$\beta > 1, \quad (5a)$$

and to 1 otherwise.

Imperfect guarding. If guarding efficiency is not perfect, so that

$$w_i = \gamma g_i + S_i \sum_j (1 - \gamma g_j),$$

where $\gamma < 1$ is the efficiency of guarding, then the invasion fitness gradient is

$$\frac{dw}{dg} = \frac{N-1}{N} \frac{\gamma - \beta - \gamma g(1 - \beta)}{1 - g}.$$

From this, one concludes that g evolves to 0 if

$$\beta > \gamma. \quad (5b)$$

and to

$$g^* = \frac{\gamma - \beta}{\gamma(1 - \beta)} \leq 1$$

otherwise.

Computing the second derivative of the invasion fitness at g^* we find that

$$\frac{d^2w}{d\tilde{g}^2} \Big|_{\tilde{g}=g} = -\frac{(1 - \beta)^2 \gamma^2 (N - 1)}{\beta(1 - \gamma)N}$$

which is always negative. Therefore, the equilibrium g^* is evolutionarily stable.

Relatedness. The above result is not qualitatively affected by the relatedness of males. The only difference is that the first factor in the right-hand side of the equation for $\frac{dw}{dg}$ becomes $(N - k)/N$ so that the rate of evolution is decreased.

Food-for-mating

In this model, each male divides his effort between provisioning females (p) and contending with other males (m) for mating opportunities, ($p + m = 1$). Provisioning at level p buys paternity in the amount γp ($0 \leq \gamma \leq 1$). Provisioning is distributed among females randomly. Provisioning increases female fertility by a factor $B(\bar{p})$. Male i fitness is

$$w_i = B(\bar{p})[\gamma p_i + S_i(1 - \gamma \bar{p})N]. \quad (6)$$

The first term in the brackets gives paternity bought with food while the second term is paternity won in competition. Note that if $\gamma = 0$ (so that provisioning does not buy any paternity), the model becomes equivalent to the communal breeding model. If $\alpha = 0$, so that $B(\bar{p}) = 1$, the model becomes equivalent to the mate guarding model.

In this model the invasion fitness gradient is $\frac{dw}{dp} = \frac{B(p)}{N(1-p^2)}H(p)$, where quadratic

$$H(p) = \gamma(\beta - 1)(N - 1)p^2 - [\alpha + \beta(1 - \gamma)(N - 1)]p + \alpha - (\beta - \gamma)(N - 1),$$

Note that $H(0) = \alpha - (\beta - \gamma)(N - 1)$, $H(1) = -2\beta(1 - \gamma)(N - 1) < 0$ and $H(0)' = -\alpha - \beta(1 - \gamma)(N - 1) < 0$.

We observe that

- If $\beta > 1$ and $\alpha < (\beta - \gamma)(N - 1)$, then $H(p) < 0$ for all p and $p \rightarrow 0$.
- If $\alpha > (\beta - \gamma)(N - 1)$, then $H(0) > 0$, $H(1) < 0$ and p evolves to an intermediate value.
- If $\beta < 1$ and $\alpha < (\beta - \gamma)(N - 1)$, then both $H(0)$ and $H(1)$ are negative. Also negative is $H(0)'$ so that no other roots are present and $H(p) < 0$. Therefore $p \rightarrow 0$.

Summarizing, if

$$\alpha < (\beta - \gamma)(N - 1),$$

then $p \rightarrow 0$. Otherwise p evolves to an intermediate value p^* given by a positive root of quadratic equation $H(p) = 0$. Assuming $\gamma = 0$ or $\alpha = 0$ simplifies the above conditions to those in the communal breeding model and in the mate guarding model, respectively, as it is supposed to.

The second derivative of the invasion fitness $\frac{d^2w}{d\bar{p}^2}|_{\bar{p}=p}$ can be found in a straightforward way but the resulting equation is rather messy. Numerical analysis however suggests that at p^* this derivative is always negative so that this equilibrium is evolutionarily stable.

There are some similarities between the behavior of this model and that in (7). (7) studied the male's dilemma regarding splitting his effort between the investments into sperm competition and into female fecundity stimulation. In their model, there are no more than 2 males ($N = 2$) and coefficient β was set to 1. According to our results, these are parameter values greatly simplifying the shift towards production. Although the models differ in many details, (7) did observe that sufficiently large α causes the males to invest exclusively in female fecundity stimulation.

Relatedness. With relatedness, the equation for H becomes

$$H(p) = \gamma(\beta - 1)(N - k)p^2 - [\alpha k + \beta(1 - \gamma)(N - k)]p + \alpha k - (\beta - \gamma)(N - k),$$

where $k = r(N - 1)$ is the number of other mutants in the group and r is relatedness. Then $p \rightarrow 0$ if

$$\alpha < \frac{(1 - r)}{1 + r(N - 1)}(\beta - \gamma)(N - 1),$$

and to an intermediate value otherwise.

Mate provisioning

Each male divides his effort between provisioning a particular female (p) and contending with other males for mating opportunities (m) ($p + m = 1$). Provisioning effort p buys γp units of paternity ($\gamma < 1$) of that female offspring and simultaneously increases her fertility by factor $B(p)$. Male i fitness is

$$w_i = B(p_i)\gamma p_i + S_i \sum_j B(p_j)(1 - \gamma p_j), \quad (7)$$

The invasion fitness is

$$w(\tilde{p}|p) = B(\tilde{p})\gamma\tilde{p} + \frac{\tilde{m}^\beta}{\tilde{m}^\beta + (N - 1)m^\beta} [B(\tilde{p})(1 - \gamma\tilde{p}) + (N - 1)B(p)(1 - \gamma p)]$$

which leads to an invasion fitness gradient in the form of $D_p = \frac{(1+p)^\alpha}{N(1-p^2)}H(p)$, where quadratic

$$H(p) = \gamma(\beta - 1 - \alpha)(N - 1)p^2 - [\alpha + \beta(1 - \gamma)(N - 1) - \alpha\gamma(N - 1)]p + \alpha - (\beta - \gamma)(N - 1),$$

Note that $H(0)$ and that $H(1)$ are the same as in the previous model. However $H'(0)$ is now $-\alpha - \beta(1 - \gamma)(N - 1) + \alpha\gamma(N - 1)$ and can be positive. Note that p can increase from very small values only if $\alpha > (\beta - \gamma)(N - 1)$ and that increasing the group size N makes it more difficult.

Assume that $\beta - \alpha - 1 > 0$. If $H(0) < 0$, then $H < 0$ for all p , and the system evolves to the state with $p = 0$ (i.e. $m = 1$). If $H(0) > 0$, then p evolves to an intermediate value p^* given by solution $H(p^*) = 0$. Let $\beta - \alpha - 1 < 0$. Then if $H(0) > 0$, p evolves to an intermediate value p^* . If $H(0) < 0$, then equation

$H(p) = 0$ has zero or two roots between 0 and 1. In the former case, $p \rightarrow 0$ always. In the later case, for small initial p , p evolves to 0 while for larger initial values p evolves to p^* which is the largest root. The threshold separating these two regimes is given by the smallest root of $H(p)$. A numerical study shows that the second regime occurs in a very narrow range of parameters.

Summarising, if

$$\alpha > (\beta - \gamma)(N - 1), \quad (8)$$

when p evolves to an intermediate value p^* . If the above condition is not satisfied, then p typically evolves to zero except that if $\beta < \alpha + 1$, there is a small range of parameter values when the system can be bistable. That is, for small initial value of p it evolves to 0 while for large enough initial values p evolves to an intermediate value. A sufficient (but not necessary) condition for evolution to $p = 0$ in this case is $H'(0) < 0$ which takes form

$$\beta > \alpha \frac{\gamma(N - 1) - 1}{(1 - \gamma)(N - 1)}.$$

With large N , this simplifies to $\beta > \alpha\gamma/(1 - \gamma)$.

Relatedness. If there is not one but k mutants per group, $H(0)$ is increased by $(\alpha + \beta - \gamma)k$ which increases the plausibility of evolving to an intermediate value of m .

Branching point and mixed strategy. Whether an intermediate equilibrium p^* is evolutionarily stable depends on the sign of the second derivative of the invasion function $\frac{d^2 w}{d\bar{p}^2}|_{\bar{p}=p}$. Although an algebraic expression for this derivative can be found in a straightforward way, it is rather messy. Numerical analysis of $\frac{d^2 w}{d\bar{p}^2}|_{\bar{p}=p}$ suggests however that depending on parameters, the equilibrium can be either stable or not. In the latter case, p^* is a branching point so that the distribution of male allele effects become dimorphic (8, 9). Numerical individual-based simulations show that in this case the system evolves to a state at which a minority of males invests exclusively in provisioning whereas the remaining males invest exclusively in mating effort. The latter males can be viewed as scroungers stealing paternity. Figure S3 illustrates the dynamics just described.

One can approximate the frequencies of males of both types. We say that a male plays strategy p if p is his efforts towards provisioning a female. Consider a resident population in which a proportion ϱ of males plays strategy 0 whereas the remaining part $1 - \varrho$ plays strategy 1. Assume there is a small frequency of mutants playing 0 and 1 with probabilities $\bar{\varrho}$ and $1 - \bar{\varrho}$, respectively. Consider fitness of a mutant in a group of size N which has n residents playing strategy 0. If the mutant plays 0, his fitness is

$$U_n = \frac{1}{n + 1} [(N - n - 1)B(1) + (n + 1)B(0)],$$

where $B(0) = 1$ and $B(1) = 2^\alpha$. If the mutant plays 1, his fitness is $V_n = B(1)$. Let

$$Q_n = \binom{N - 1}{n} \varrho^n (1 - \varrho)^{N - n - 1}$$

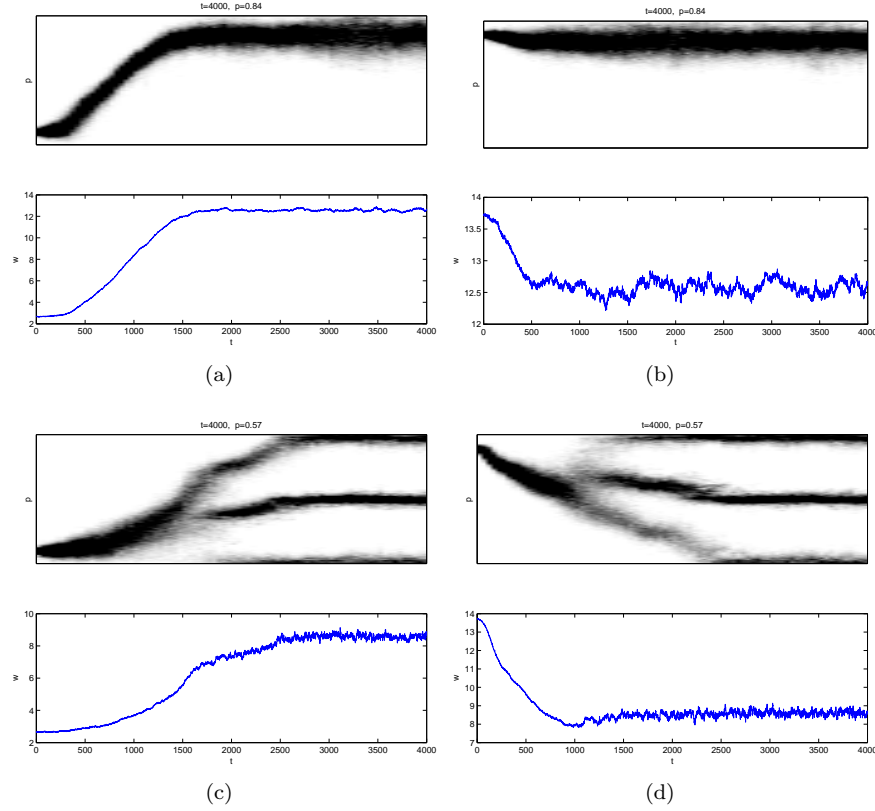


Figure S3: Examples of evolutionary dynamics during 4000 generations. (a) and (b): Evolution towards an ESS. Two runs with different initial conditions. Parameters: $N = 8, \alpha = 3, \beta = 1, \gamma = 0.8, \mu = 0.001$. (c) and (d): Evolution towards a branching point with subsequent divergence. Two runs with different initial conditions. Parameters the same as in (a) and (b) except that $\gamma = 0.6$. Shown are the distribution of the provisioning trait using gray scale (top) and the average female fertility (bottom). In the case of branching, the distribution of the allelic effects is bimodal, but the phenotypic distribution (as shown) is trimodal because individuals are diploid.

be the probability that in the group there are n residents playing 0. [This assumes that the groups are formed randomly.] Then the invasion fitness is

$$w(\tilde{\varrho}|\varrho) = \sum_{i=0}^{N-1} Q_n \tilde{\varrho} \frac{(N-n-1)B(1) + (n+1)B(0)}{n+1} + (1-\tilde{\varrho})Q_n B(1).$$

After simplifications, the selection gradient is

$$\frac{\partial w(\tilde{\varrho}|\varrho)}{\partial \tilde{\varrho}} \Big|_{\tilde{\varrho}=\varrho} = \frac{B(1)[1 - (1-\varrho)^N] - (2B(1) - 1)\varrho}{\varrho}.$$

From here we conclude that the frequency of males paying strategy 0 is approximately

$$\varrho^* \approx \frac{B(1)}{2B(1) - 1}$$

which is asymptotically approaching 1/2 from above as $B(1) \rightarrow \infty$. Note that the existence of the mixed equilibrium does not depend on β . Presumably, β affects its stability.

A summary on the effects of relatedness

The kin selection theory (10, 11, 12) predicts reduced competition in kin groups. This is indeed what happens in the communal care, food-for-mating and mate provisioning models. Specifically, with average genetic relatedness in the group, r , the right-hand side of the inequalities in Table 1 must be multiplied by factor $\frac{1-r}{1+r(N-1)}$ which is < 1 . Relatedness thus weakens the conditions for escaping the state with $m = 1$. (In the mate guarding model, relatedness has no effect.) However with realistically small values of r , the conditions given in Table 1 will not change substantially. (For example, if half of the group offspring disperses randomly while the rest stay in the native group, $r \approx 4/(3N)$ (6).)

Pair-bonding

The pair bonding model has three additional components not yet consider in the models above. These are female faithfulness, cost of monogamy, and assortative pair-bond formation. We consider these components separately.

Female faithfulness. Females can be to some extent faithful to the males that provision them. Let f_i be the faithfulness of the female i . Male fitness w_i above can be rewritten as

$$w_i = B(p_i)\mathcal{P}_i + S_i \sum_j B(p_j)(1 - \mathcal{P}_i), \quad (9)$$

with male paternity of the provisioned female offspring $\mathcal{P}_i = \gamma p_j$. Introducing female faithfulness f we can generalize \mathcal{P}_i to

$$\mathcal{P}(p_i, f_i) = 1 - (1 - f_i)(1 - \gamma p_j).$$

Note that paternity is $\mathcal{P} = 1$ if the female is completely faithful, $f_i = 1$. If $f_i = 0$, we recover $\mathcal{P}_i = \gamma p_j$. For the pair-bonding model, the terms $H(0)$, $H(1)$ and $H'(0)$ above change to

$$\begin{aligned} H(0) &= [1 + f(N - 1)]\alpha - (1 - f)(\beta - \gamma)(N - 1), \\ H(1) &= -2\beta(1 - f)(1 - \gamma)(N - 1) < 0, \\ H'(0) &= -\alpha[1 + r(N - 1) + (1 - r)\gamma(N - 1)] - (1 - r)\beta(1 - \gamma)(N - 1) \end{aligned}$$

Now evolution towards intermediate value of p requires

$$\alpha > \frac{1 - f}{1 + f(N - 1)} (\beta - \gamma)(N - 1), \quad (10)$$

That is increasing female faithfulness f increases the plausibility of an intermediate equilibrium.

Benefit of promiscuity. Under many conditions females benefit from mating with multiple males (13, 14, 15, 16, 17, 18). We can capture this by assuming that female fertility declines as paternity P of her mate increases. This can be described by the following substitution in the model equations

$$B(p_i) \rightarrow B(p_i)C_i,$$

where $C_i = 1 - \varepsilon\mathcal{P}_i^k$ captures the cost of monogamy with ε being the maximum decline in fertility and k being a positive parameter. Then the male fitness becomes

$$w_i = \mathcal{B}(p_i)\mathcal{P}_i + S_i \sum_j \mathcal{B}(p_j)(1 - \mathcal{P}_j). \quad (11)$$

where $\mathcal{B}(p_i) = B(p_i)C_i$ is female fertility.

Sexual selection on faithfulness. We write the expected fitness of a female with faithfulness f in a population with some distribution of the male provisioning trait p as

$$w(f) = \mathbb{E}_p \left\{ B(p)C(f, p) \frac{\psi(f, p)}{\mathbb{E}_f \{\psi(f, p)\}} \right\}$$

where the outside expectation is taken over all males, the inside expectation is taken over all females in the group, and the ratio is the probability of $f \times p$ pairing. Assuming that the variation in f and p is small, $w(f)$ can be approximated as

$$w(f) \approx B(\bar{p})[1 - \varepsilon\mathcal{P}(f, \bar{p})^k] \frac{\psi(f, \bar{p})}{\psi(\bar{f}, \bar{p})} = B(\bar{p})[1 - \varepsilon\mathcal{P}(f, \bar{p})^k] \exp(\omega(f - \bar{f})\bar{p}),$$

where \bar{f} and \bar{p} are the corresponding mean values. From here and using $\mathcal{P}(f, p) = 1 - (1 - f)(1 - \gamma p)$, the invasion fitness gradient at $f = 0$ is

$$D_f = B(p) [\omega p - (\gamma p)^{k-1} (k + \omega \gamma p^2 - k \gamma p)].$$

With $k = 4$ and small p , this is approximately $B(p)p(\omega - 4\varepsilon\gamma^3 p^2)$. Assuming that p is maintained at some low level (e.g. by a mutation-selection-drift balance), $f = 0$ is locally stable if

$$\varepsilon > \frac{\omega}{4\gamma^3 p^2},$$

that is, if the advantage of promiscuity is sufficiently large.

Numerical simulations

In numerical simulations, male- (p) and female-expressed (f) traits were controlled by two unlinked additive autosomal loci with a continuum of alleles produced by mutation. The following is a list of parameter value varied in simulations: $N = 4, 8, 16$; $\alpha = 0.5, 1.0, 2.0$; $\beta = 2, 3, 4$; $\gamma = 0.25, 0.50, 0.75$; $\sigma = 0.25, 0.50, 1.00$; $\omega = 0.5, 1.0, 2.0$; $\varepsilon = 0, 0.05, 0.10$. The mutation rate per gene per generation was 10^{-3} , the effects of mutations were chosen from a uniform distribution on interval $[-0.05, 0.05]$. Given a mutation, p values at all ranks were modified independently. There were $G = 400$ groups. Male offspring stayed in the native group while females dispersed randomly. Selection was hard with the expected number of offspring of a female set to $2(1.02 + \varepsilon)B$. The actual offspring number was determined using a stochastic variance-reduction procedure analogous to that in Ref.(5). I also enforced an equal number of daughters and sons for each female.

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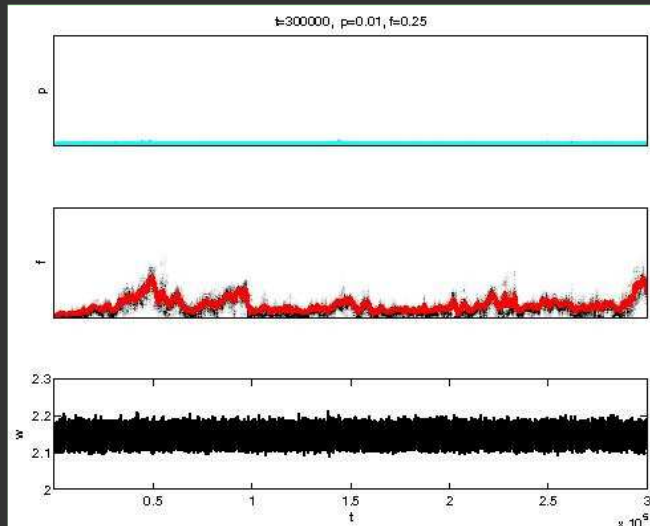
Image gallery

The figures to follow illustrate the dynamics observed in numerical simulations for a sample of parameter combinations. The parameter values are shown under each graph. For example, N4.a0.5b3.0g0.25.o1.00.s0.e0.05.1.eps means that $N = 4$, $\alpha = 0.5$, $\beta = 3.0$, $\gamma = 0.25$, $\omega = 1.00$, $\sigma = 0.25$ and $\varepsilon = 0.05$. (The last number 1 should be ignored.) On top of each graph I show the final generation t as well as the average values of p and f traits across the population at the last generation.

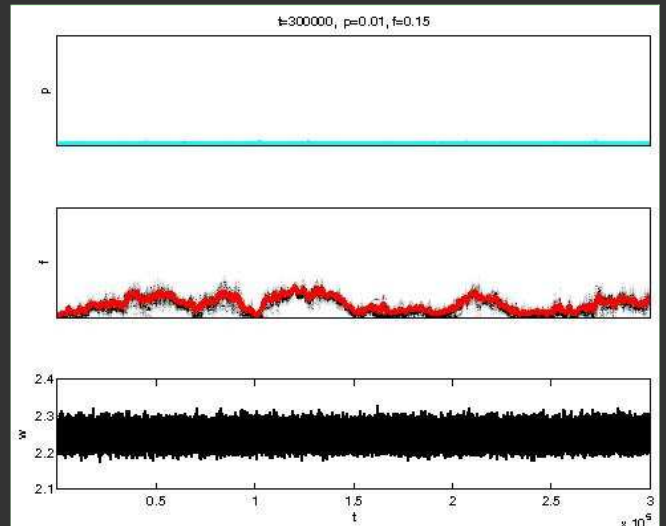
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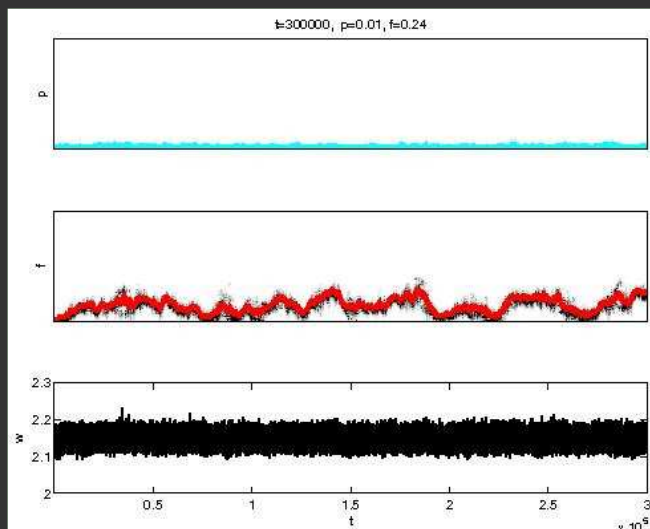
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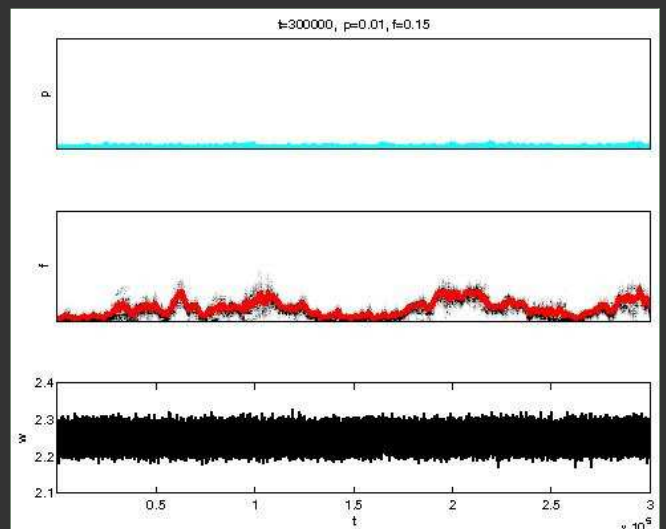
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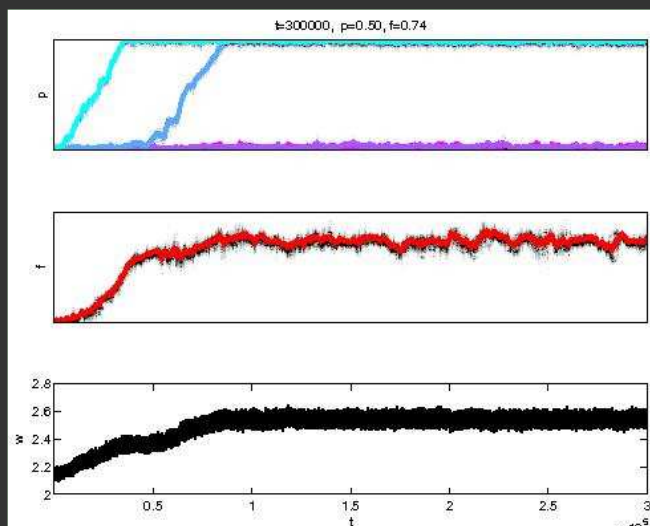
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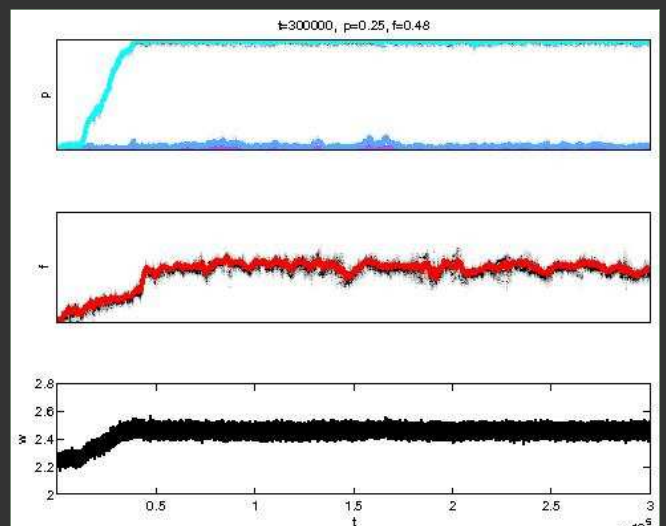
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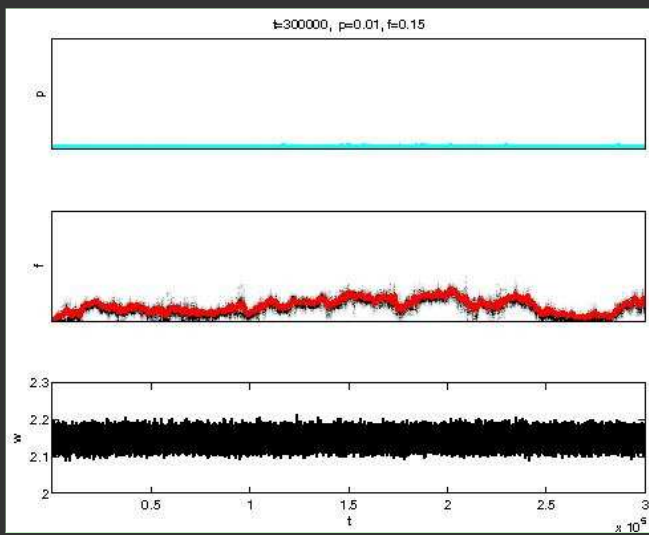
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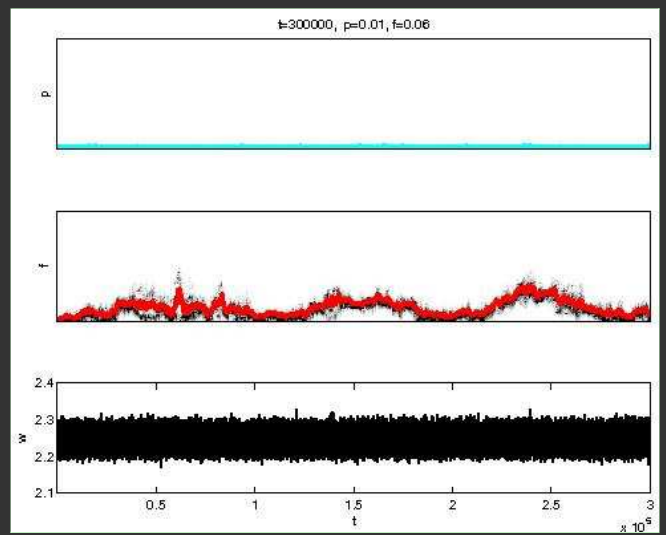
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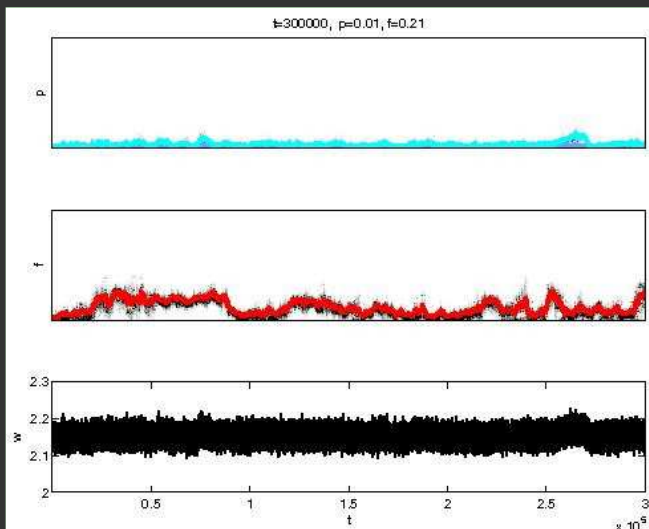
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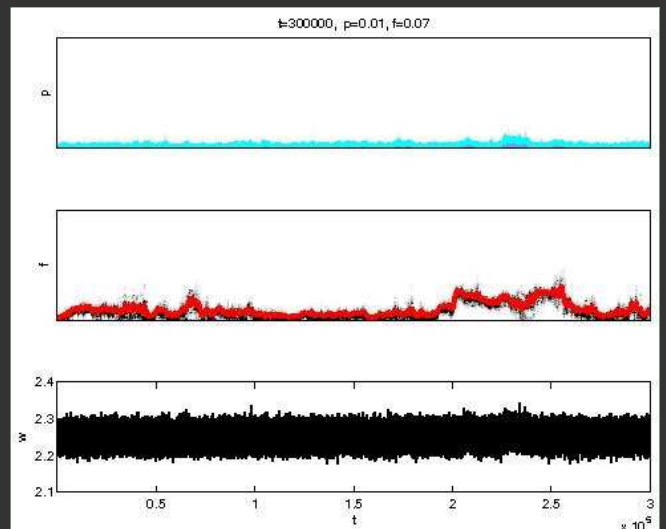
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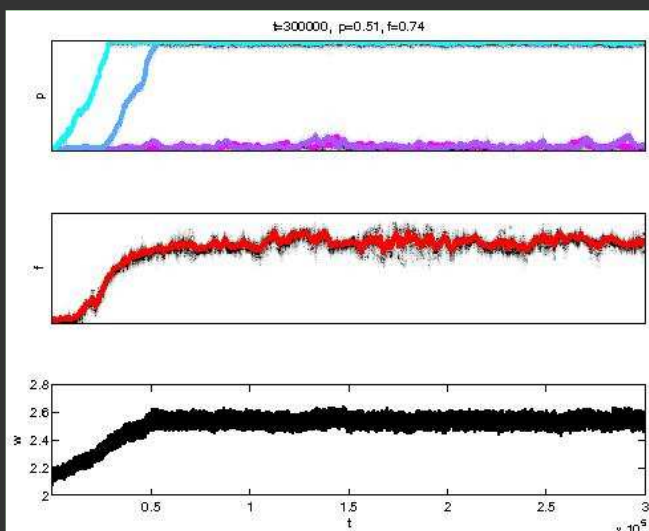
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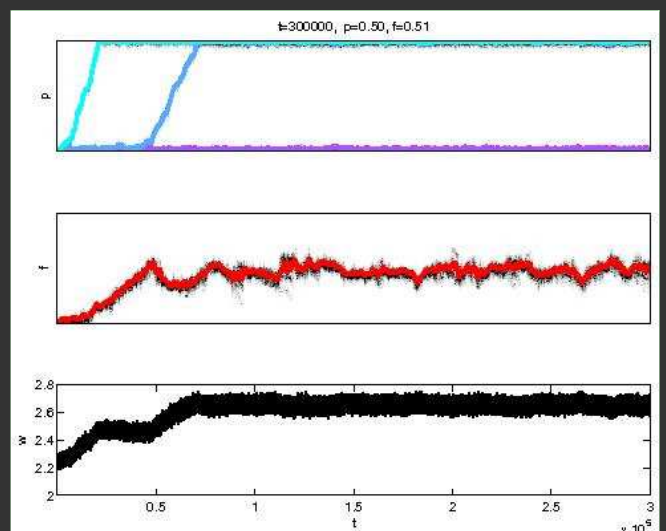
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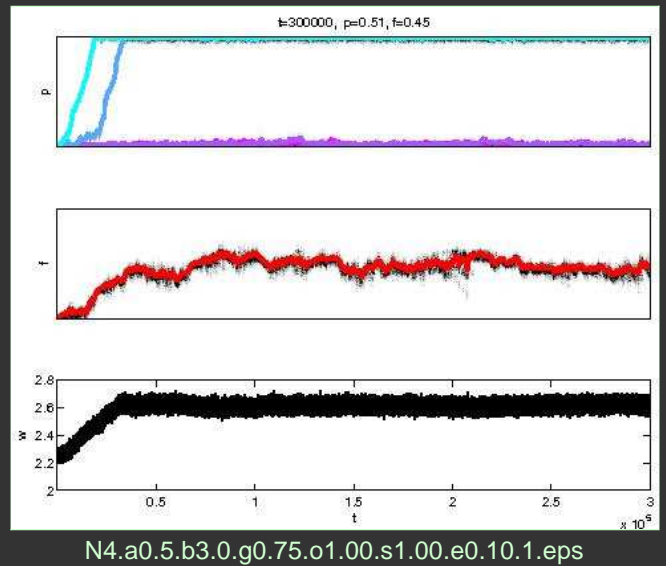
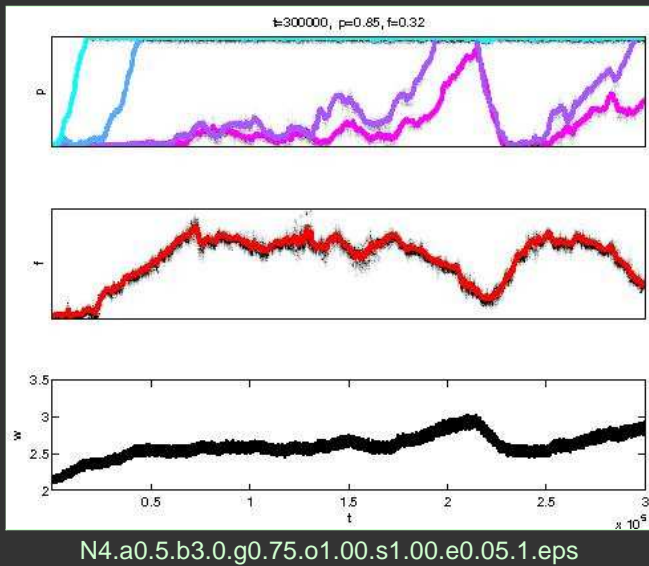
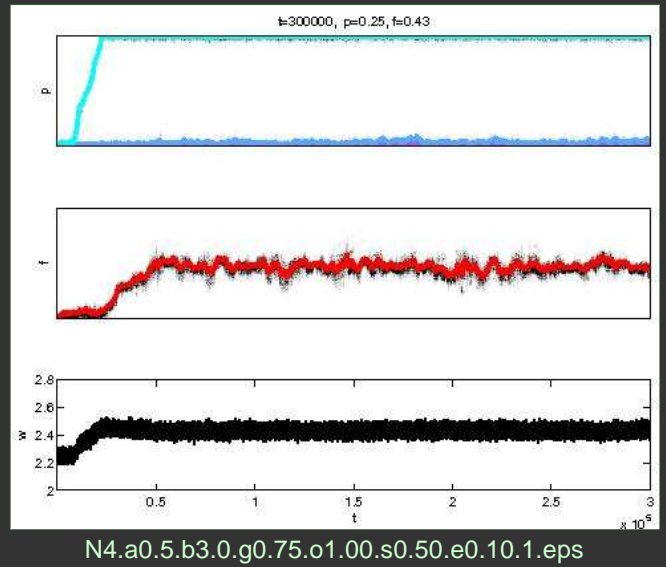
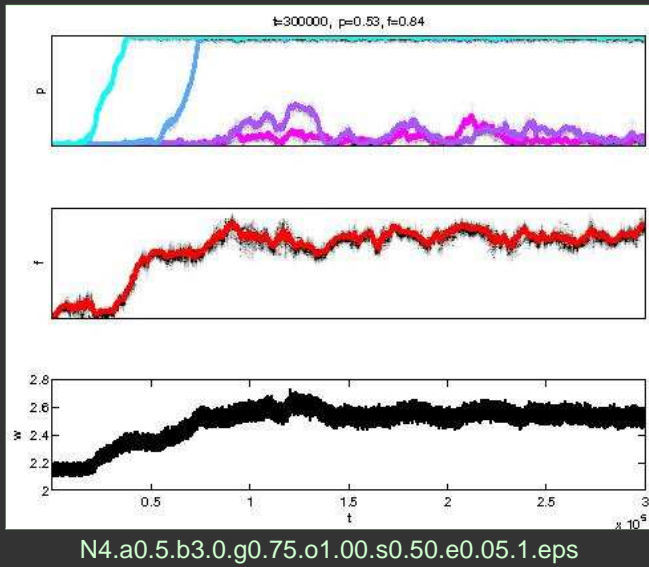
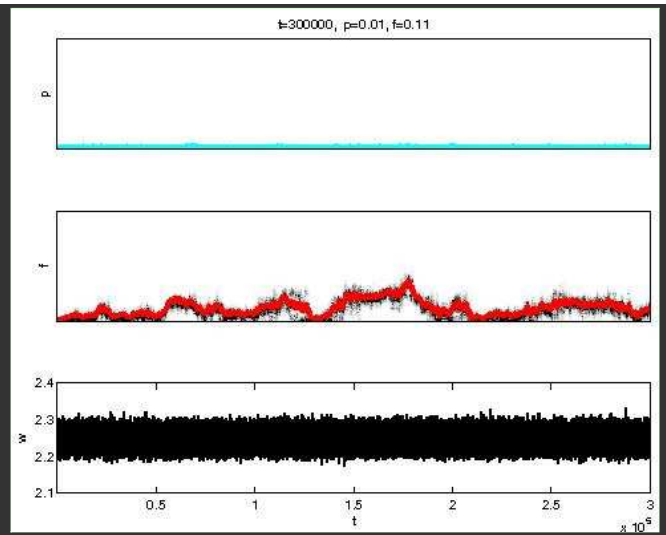
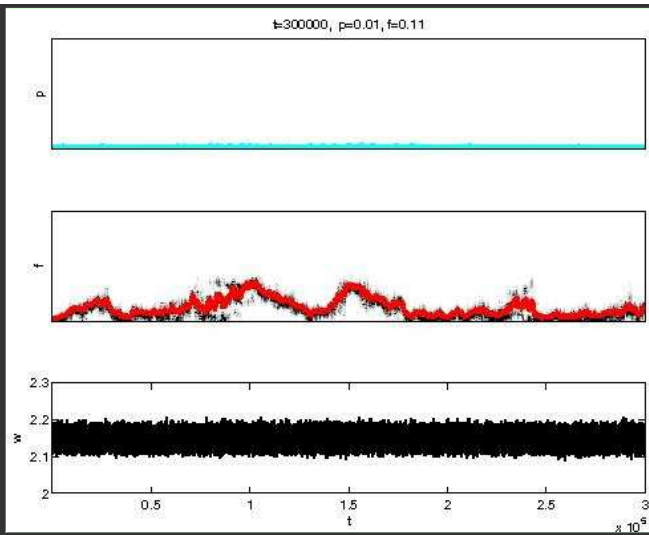
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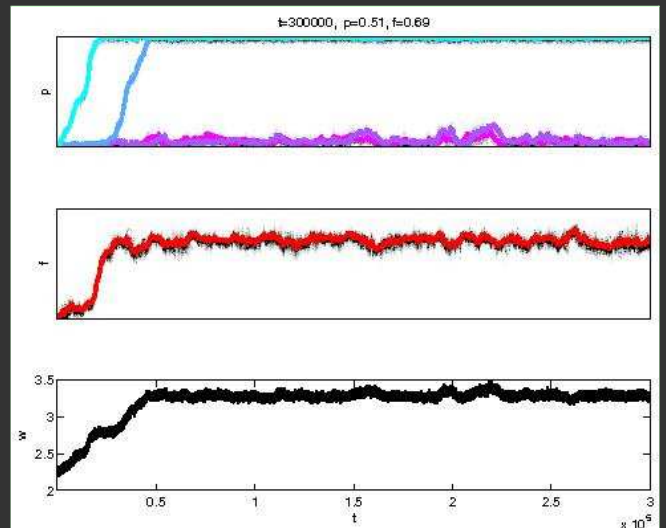
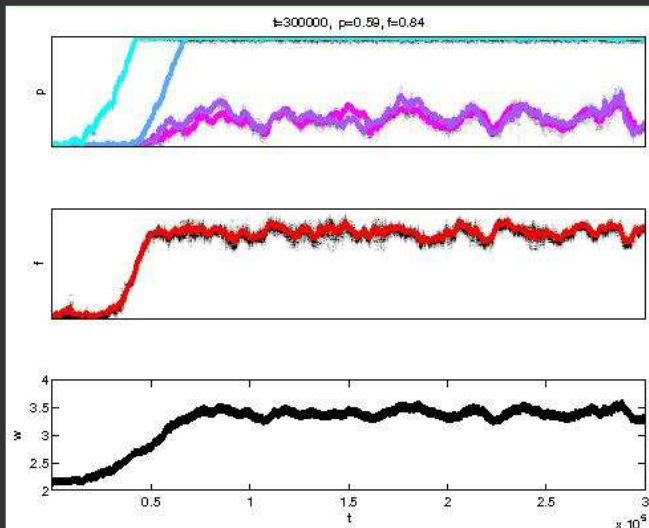
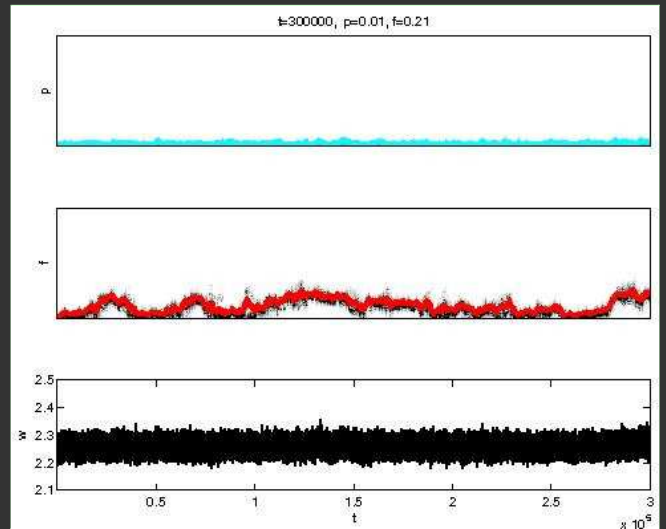
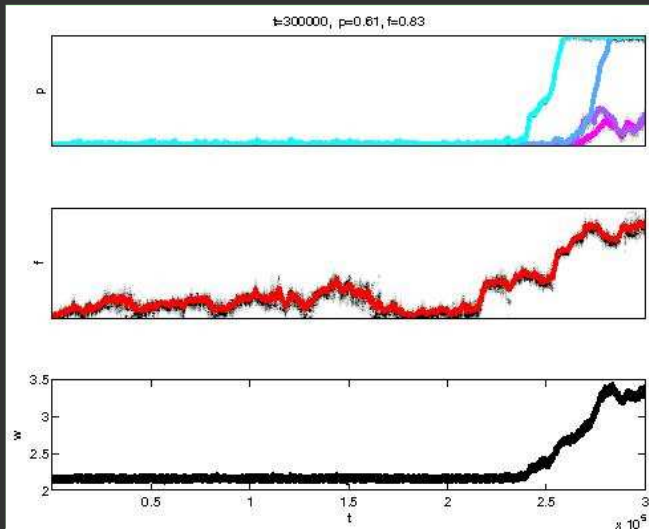
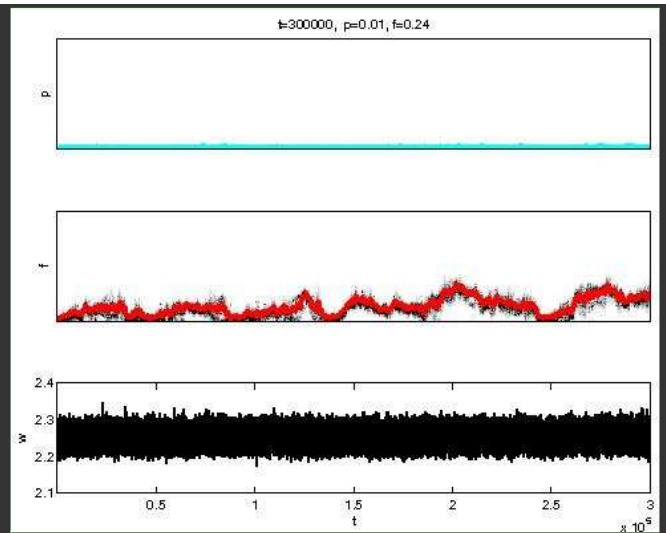
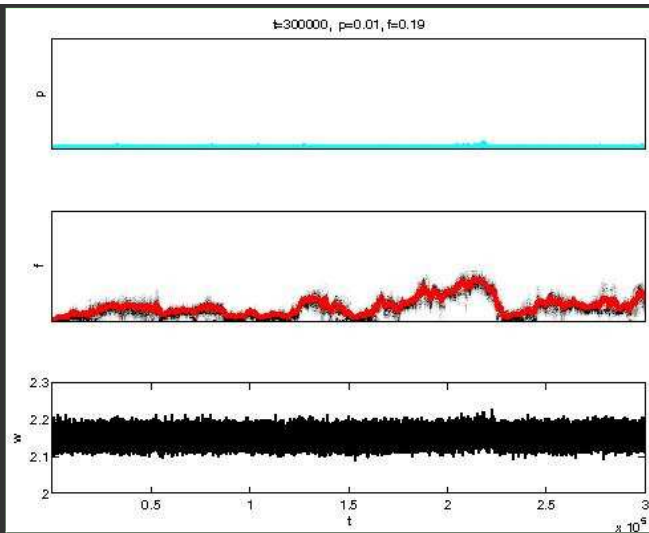


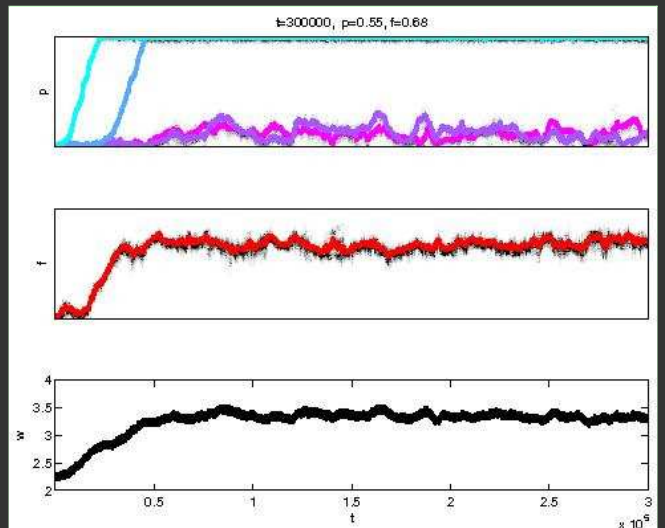
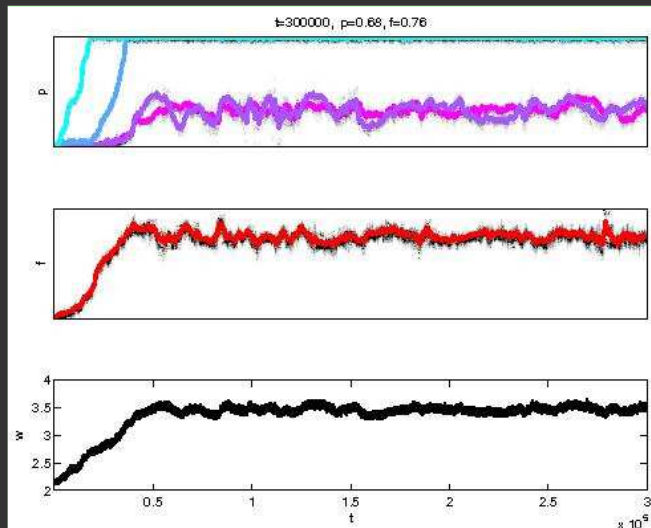
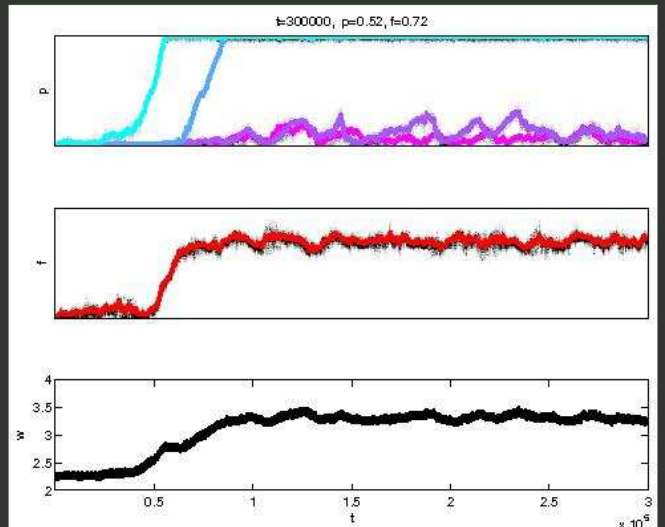
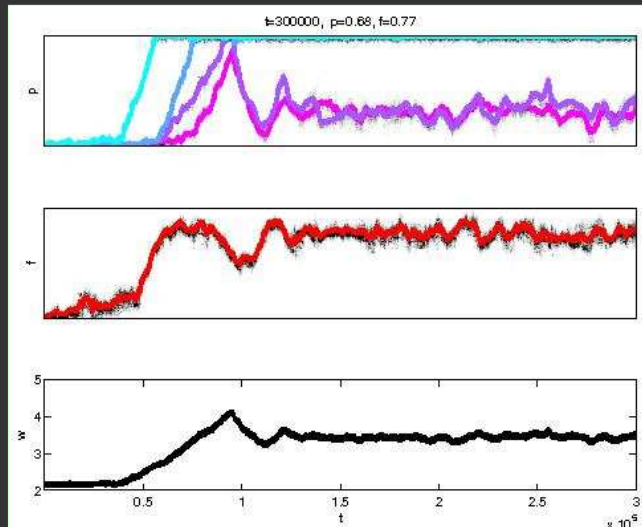
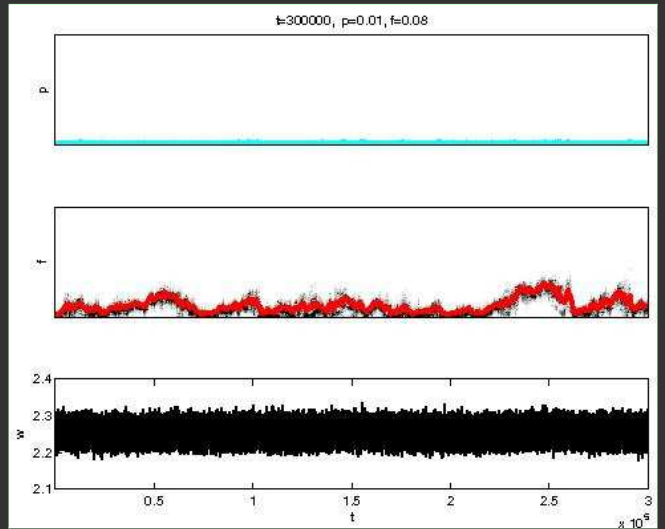
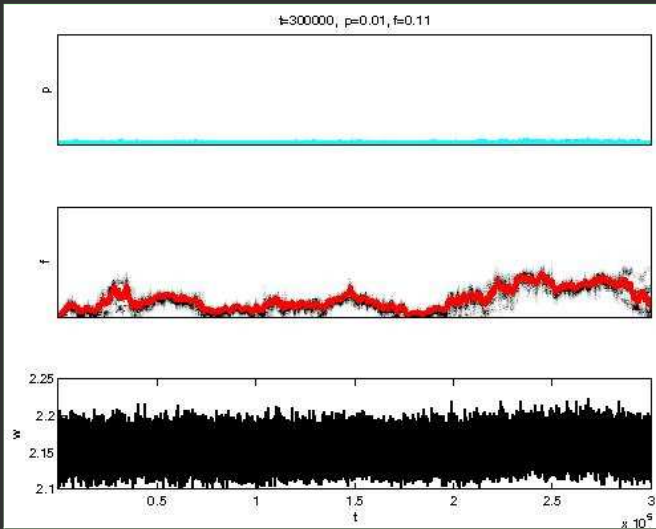
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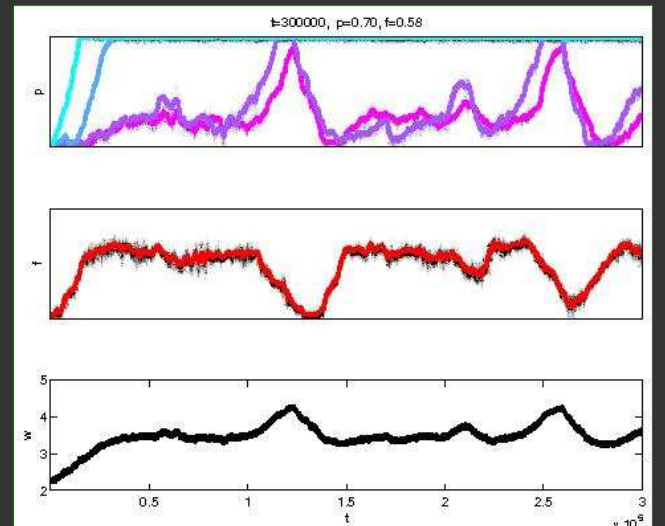
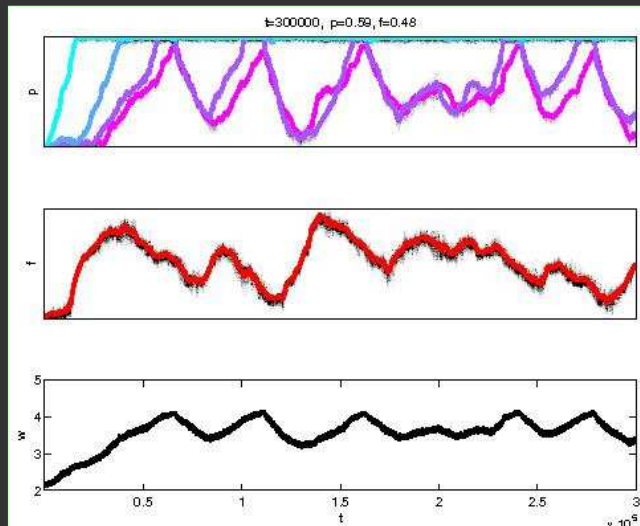
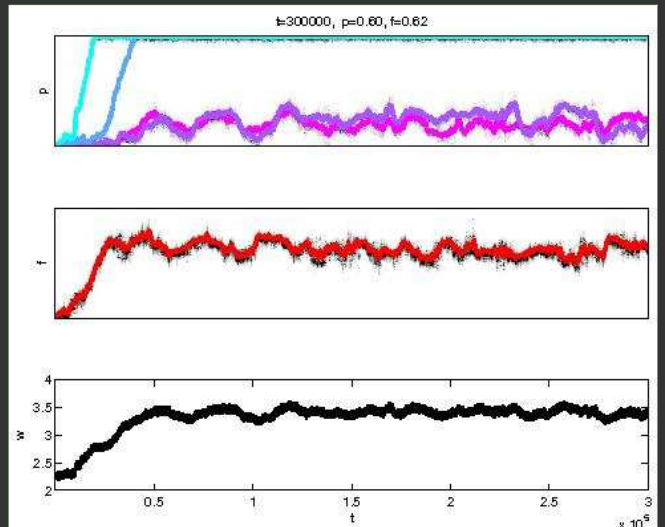
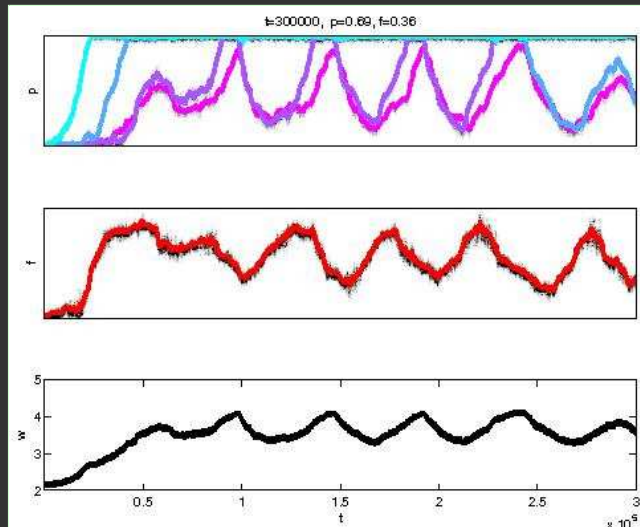
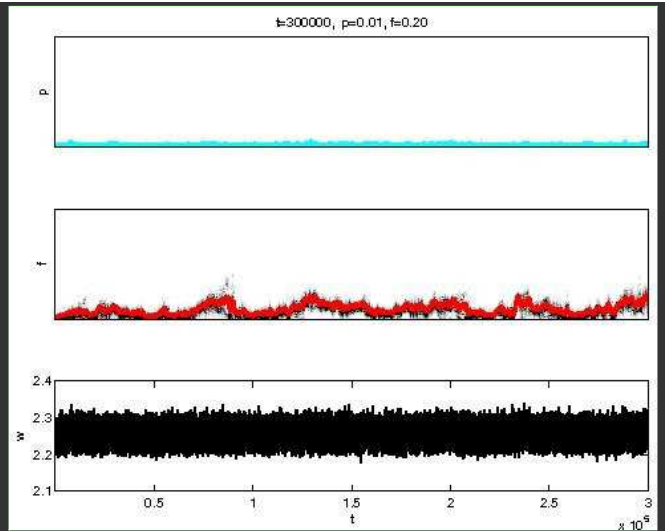
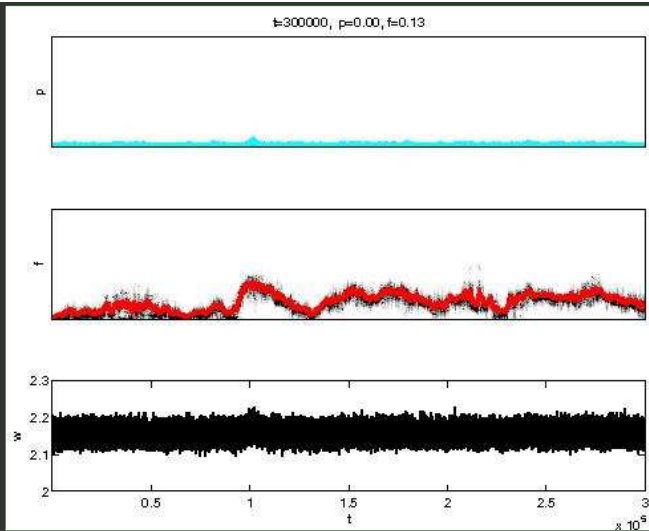


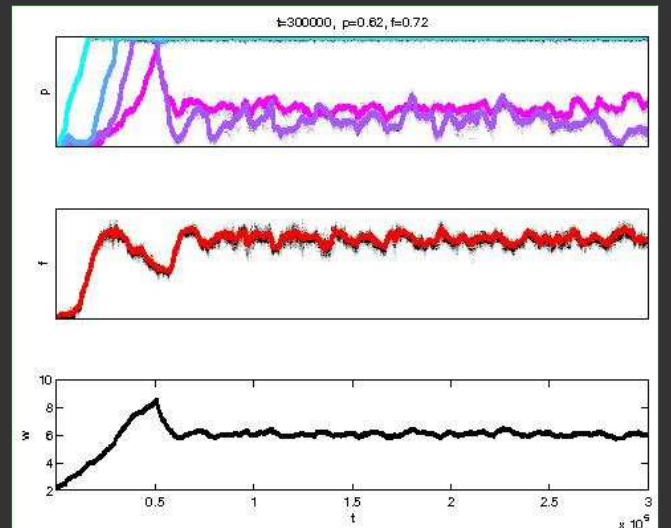
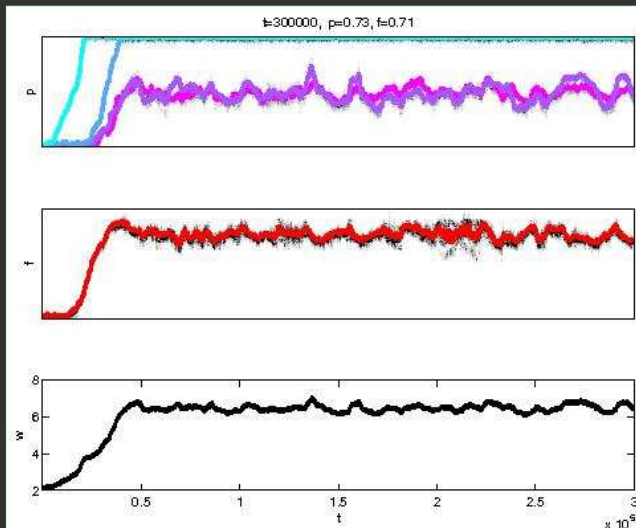
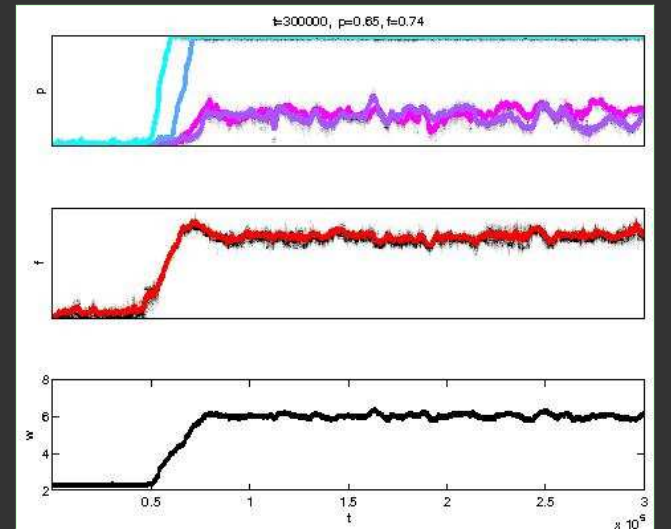
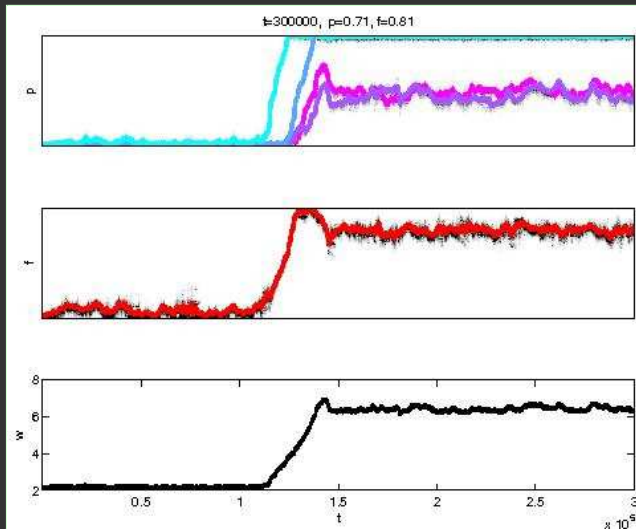
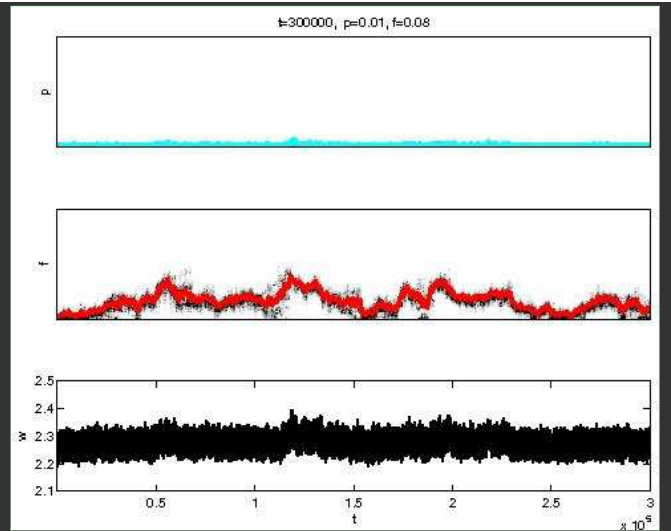
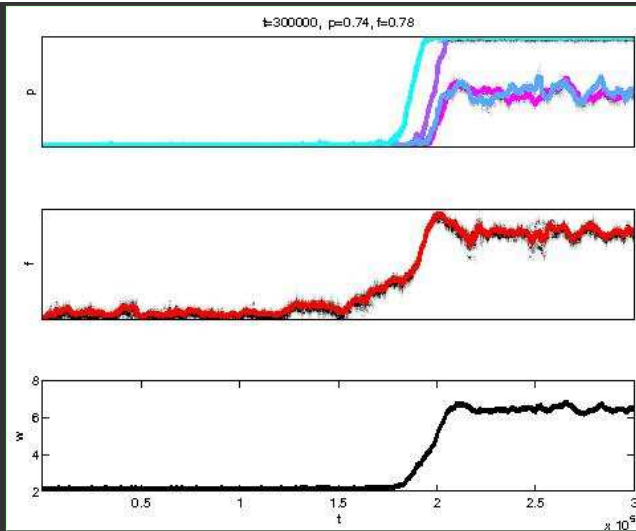
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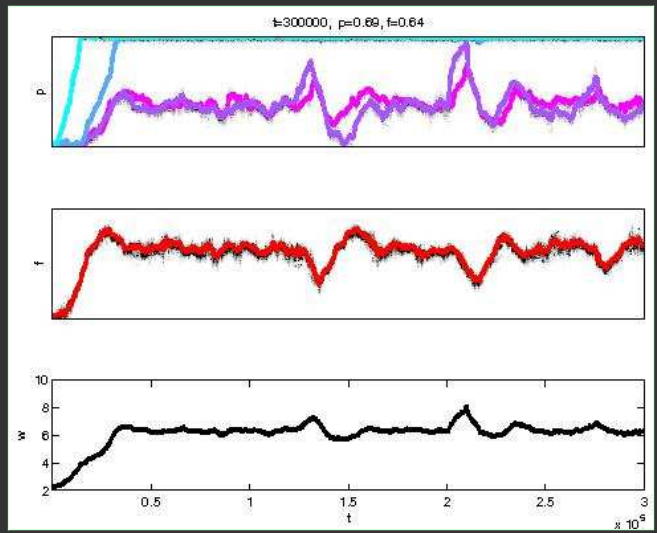
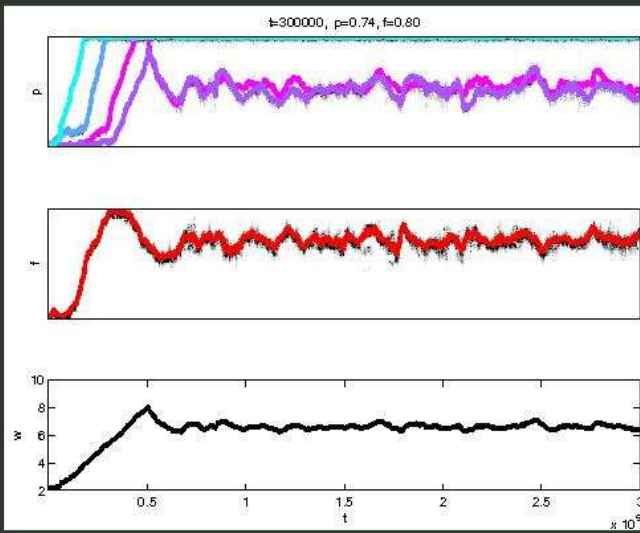
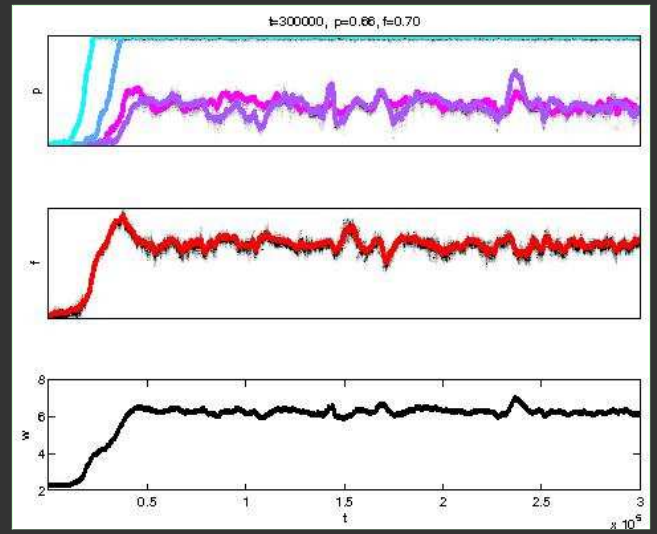
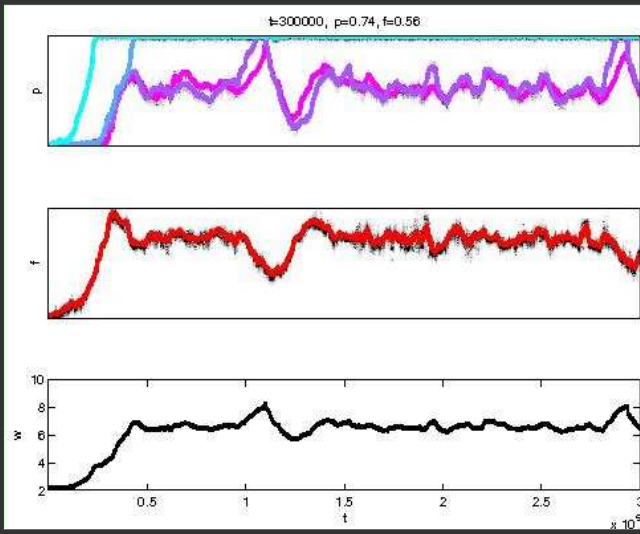
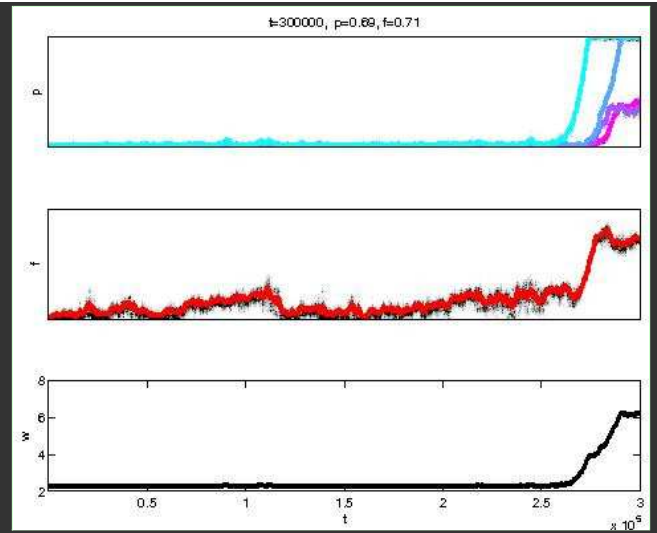
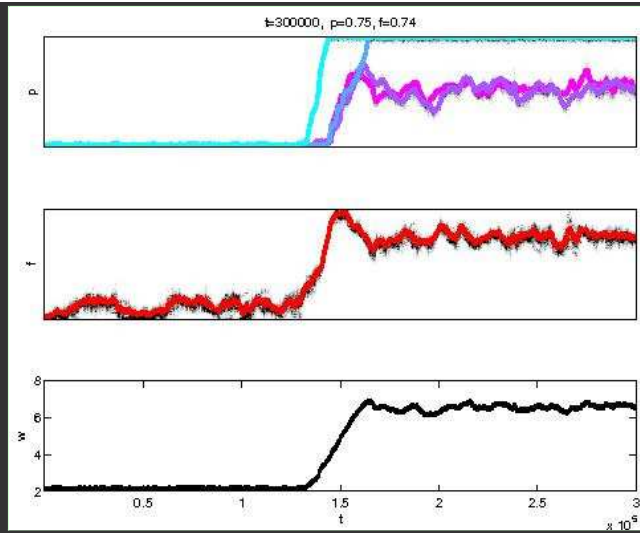












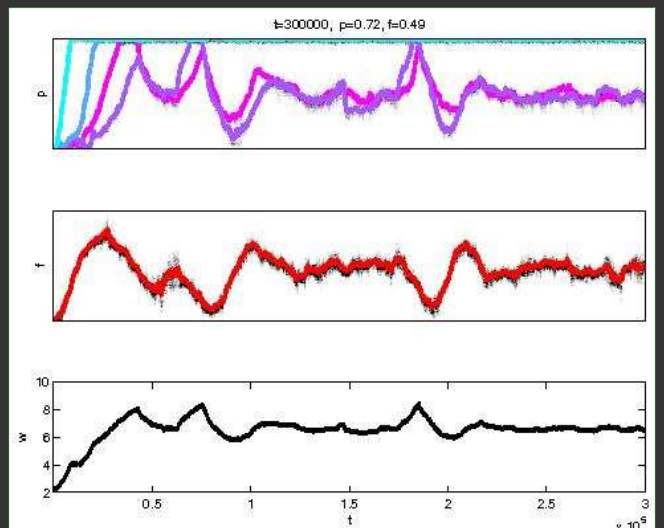
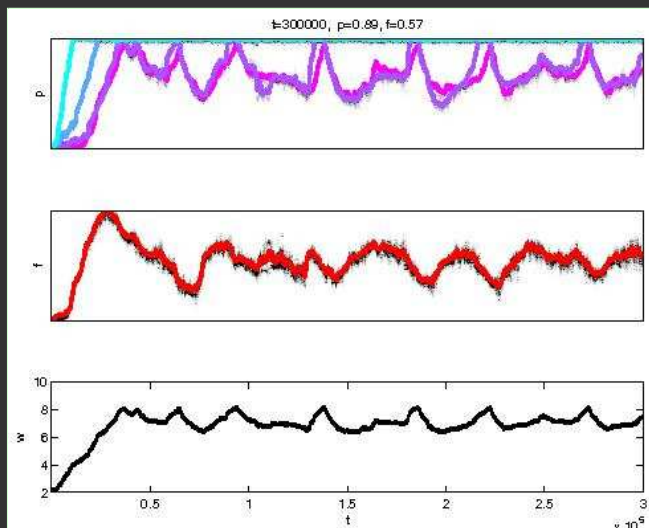
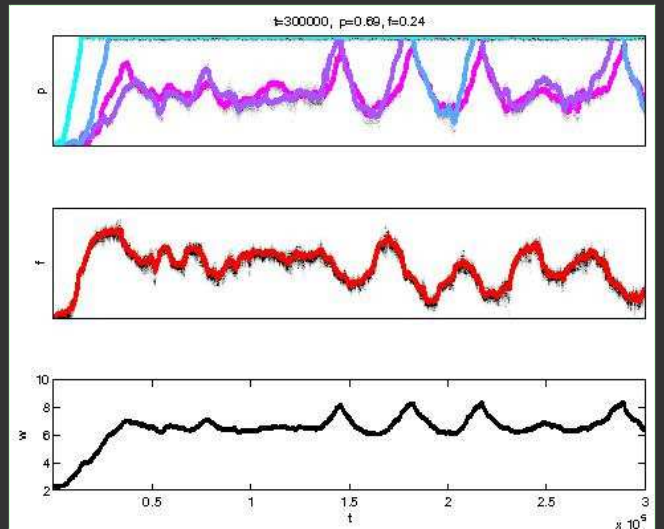
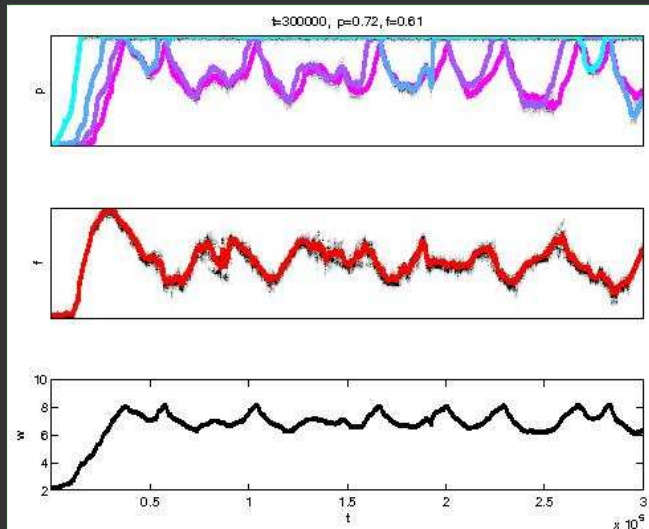
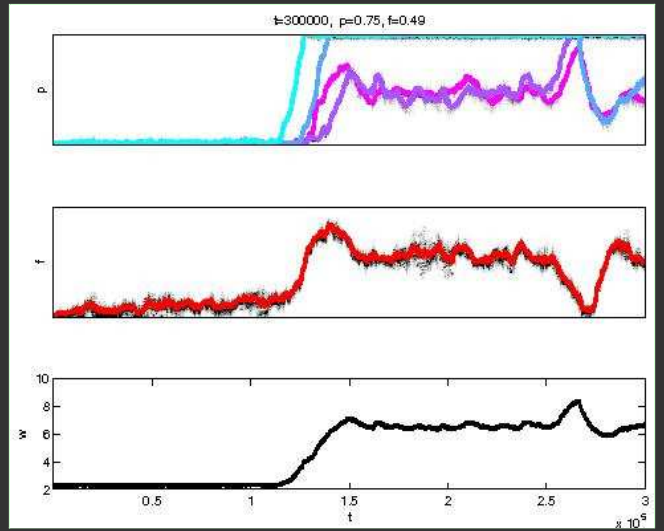
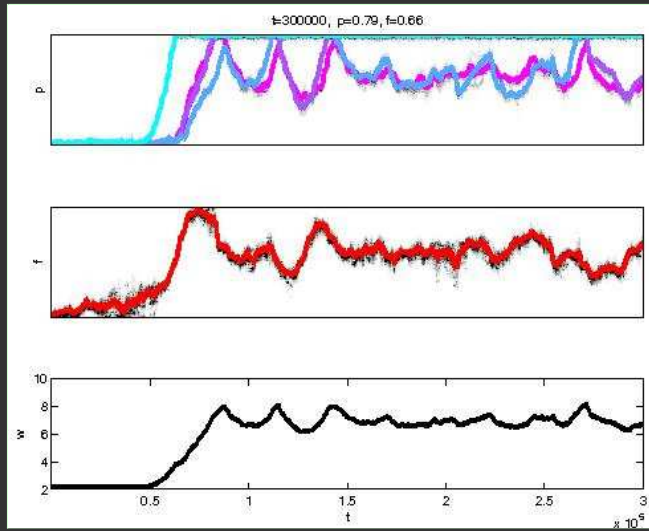
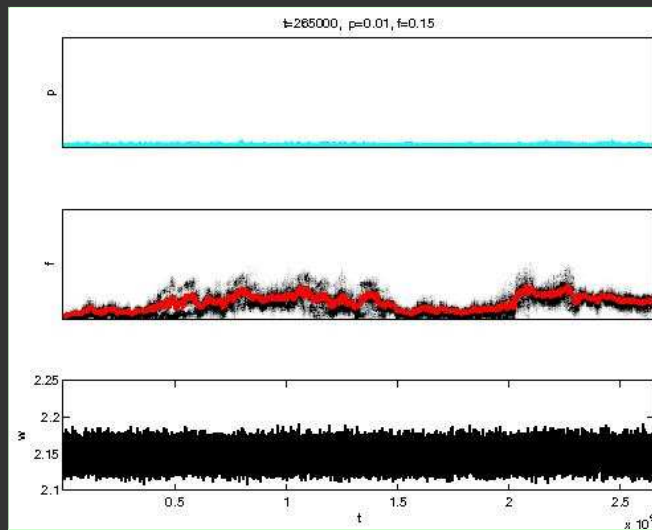


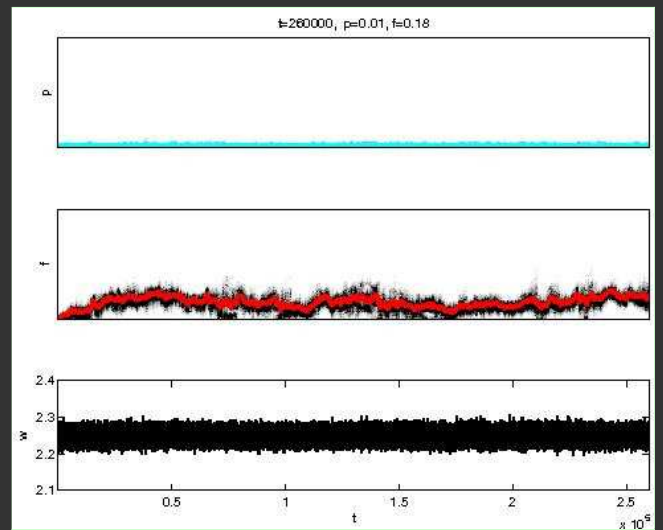
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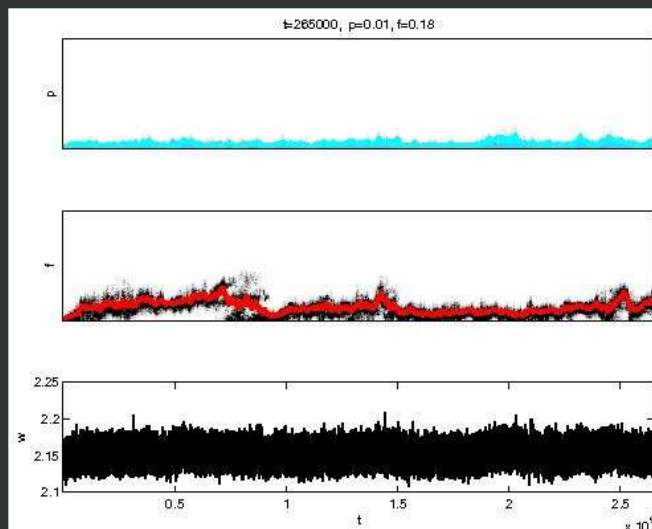
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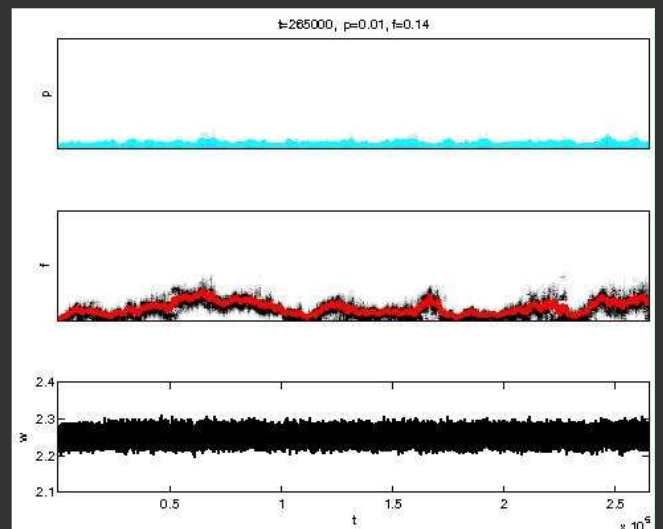
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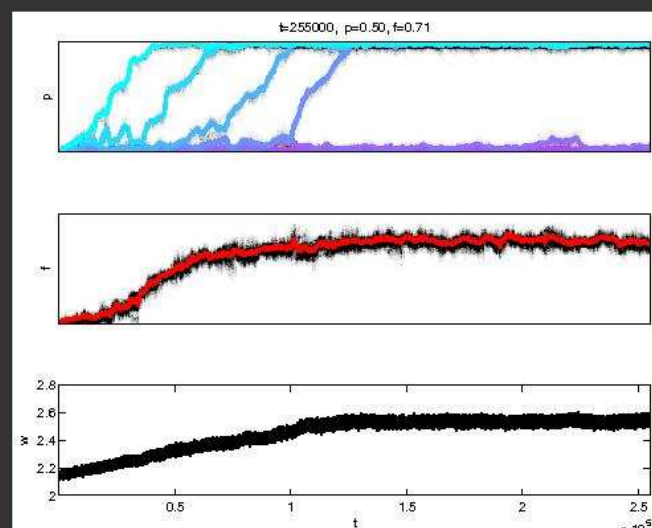
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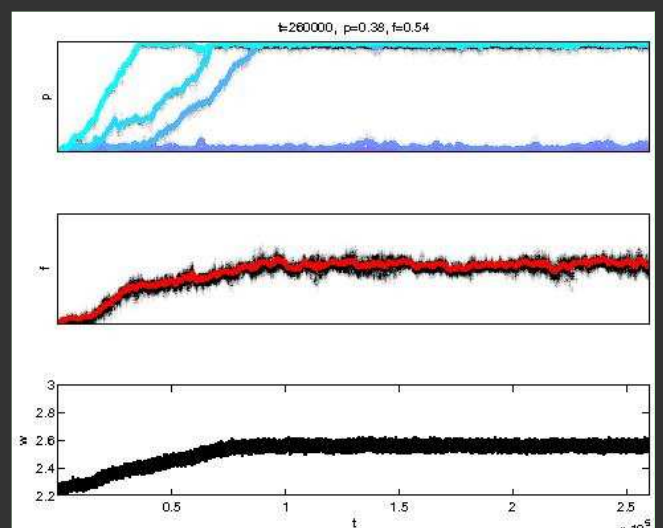
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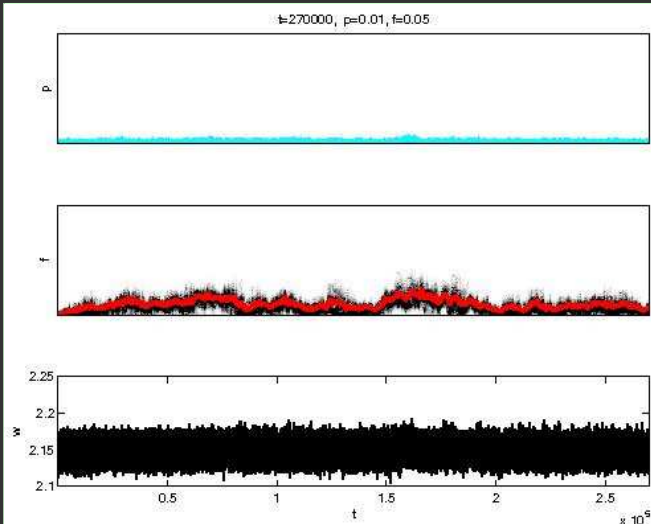
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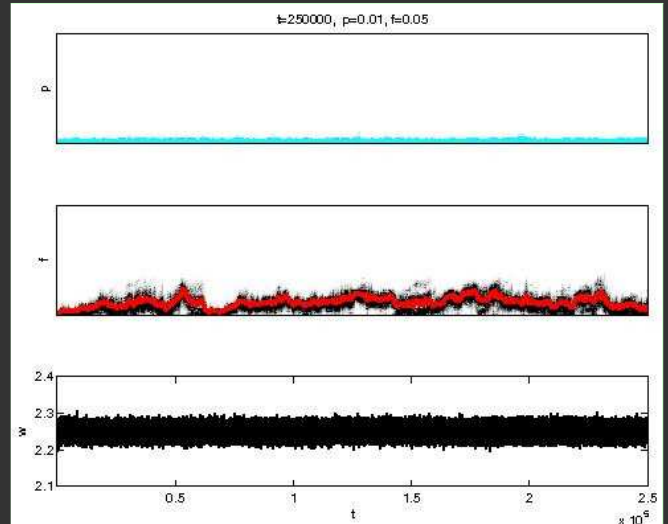
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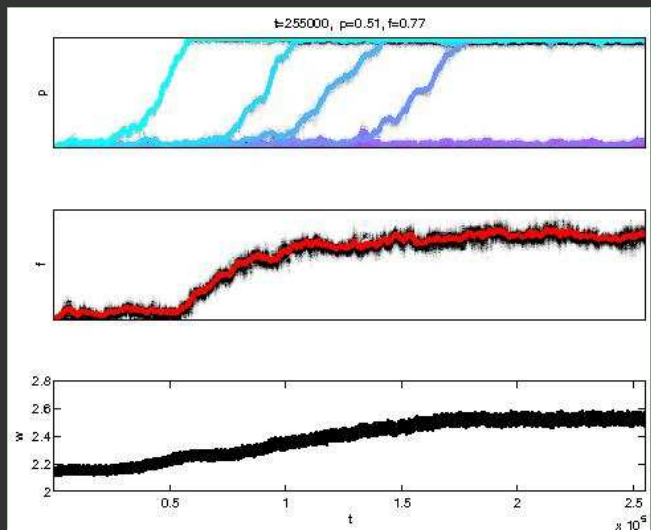
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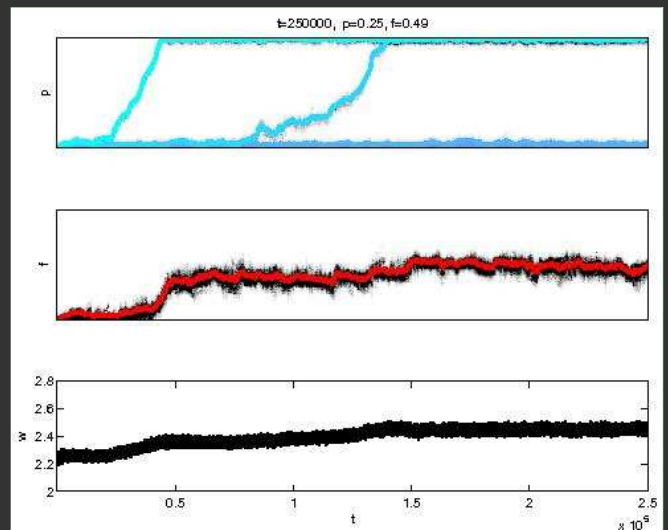
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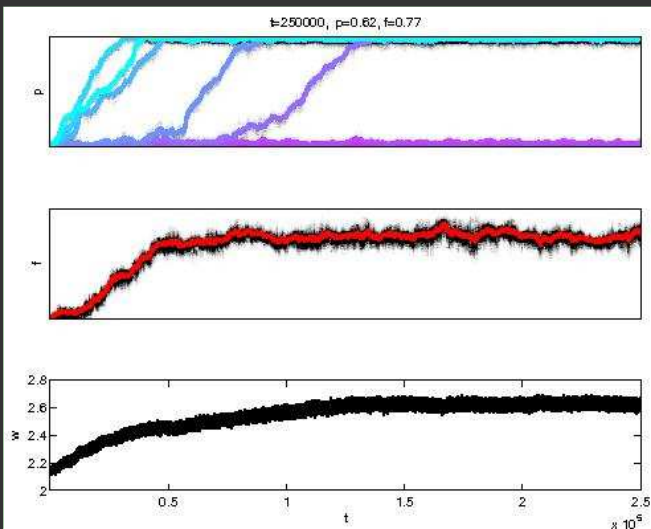
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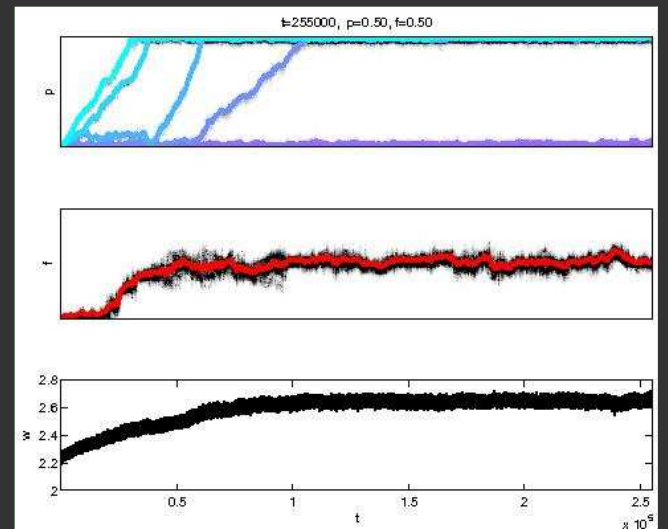
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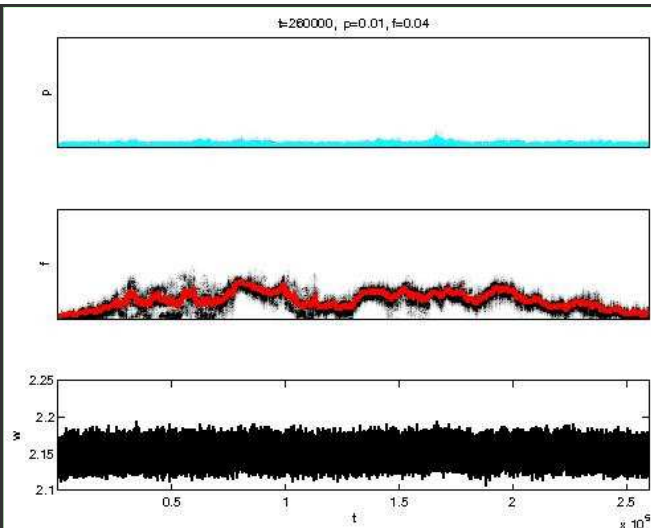
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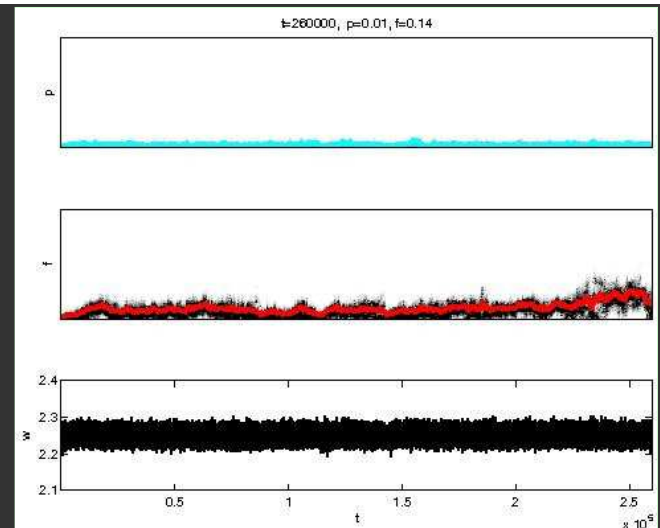
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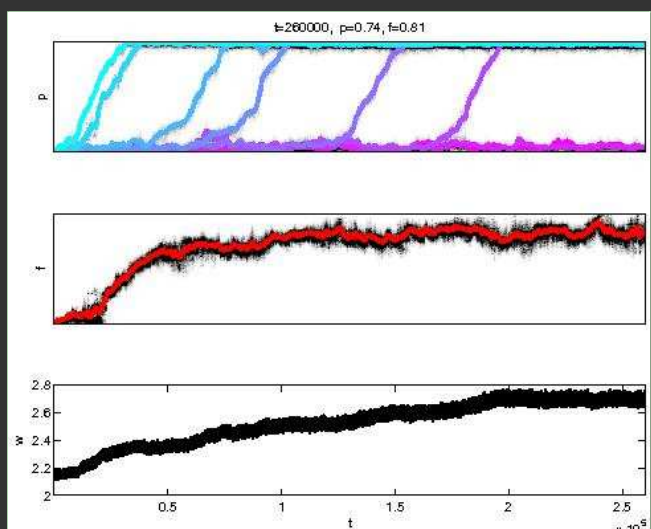
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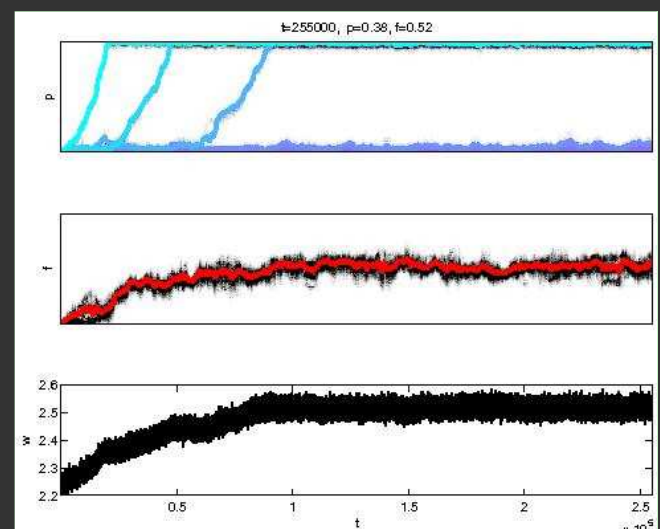
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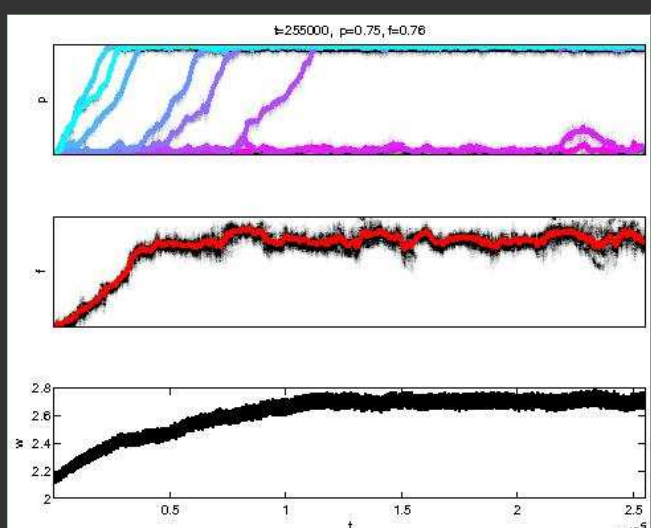
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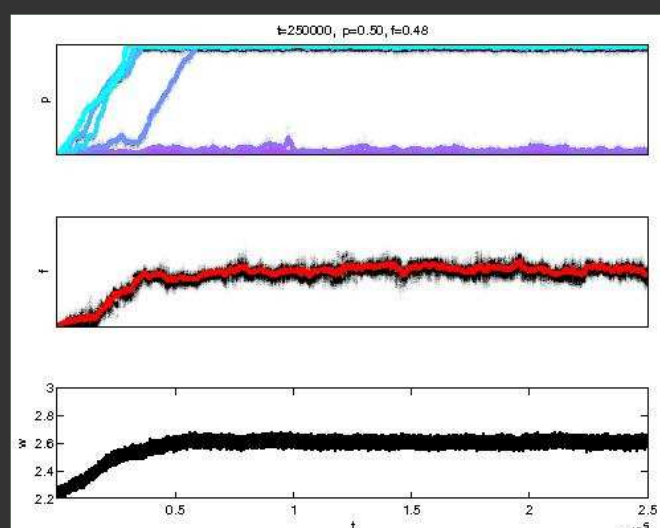
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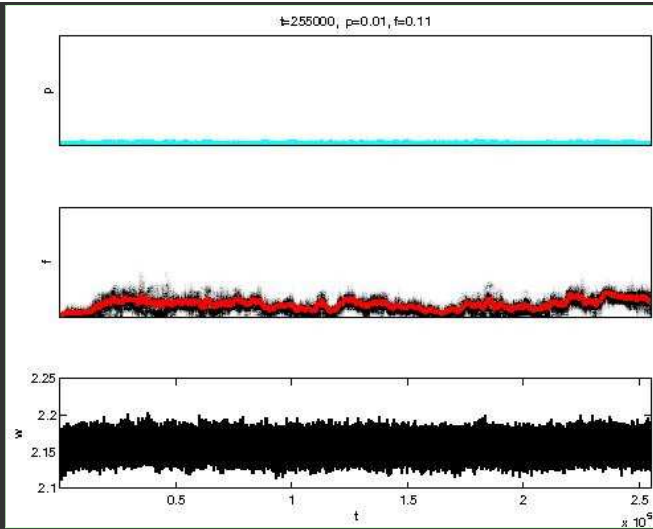
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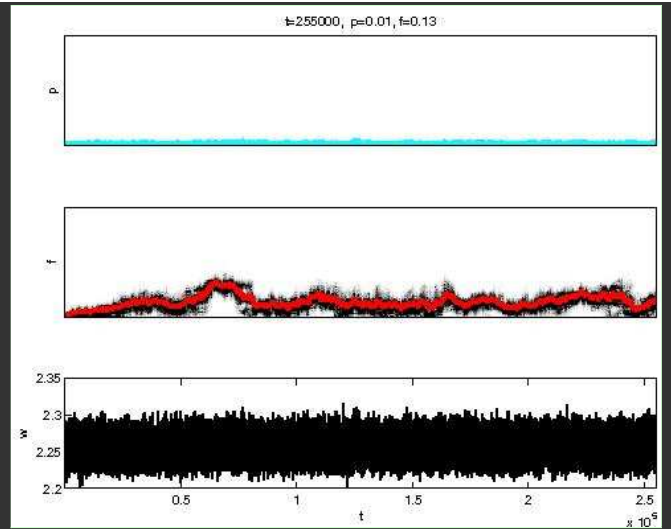
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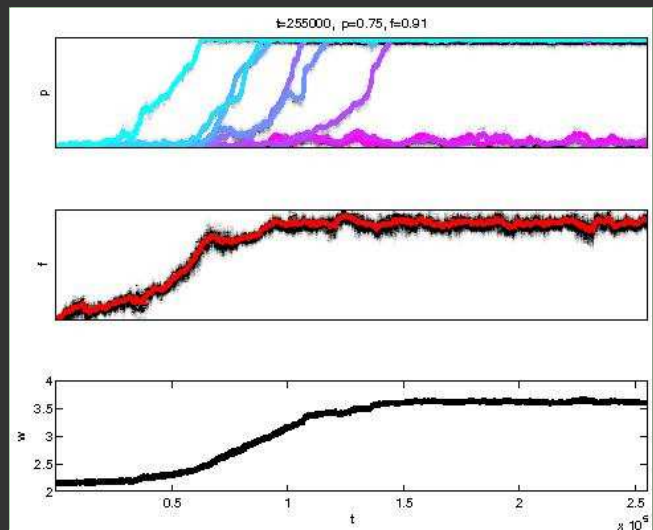
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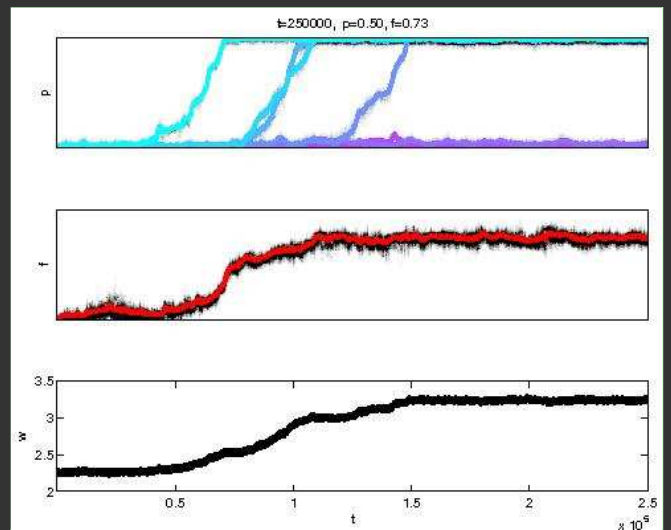
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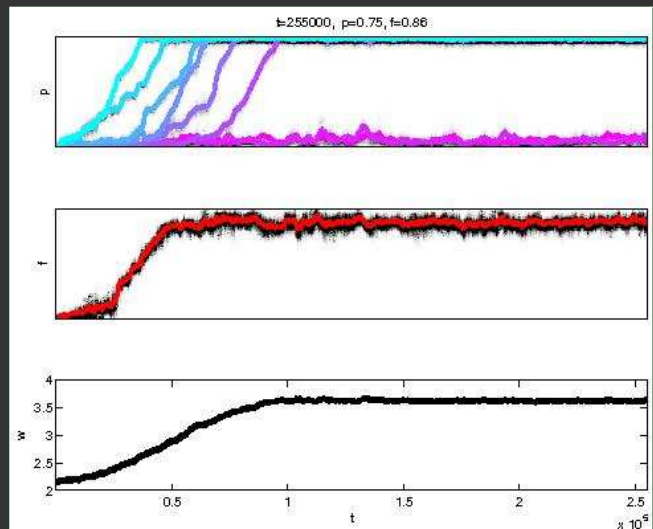
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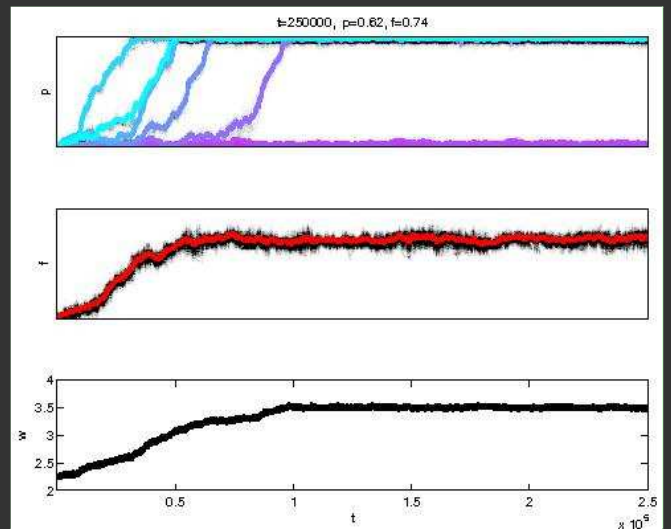
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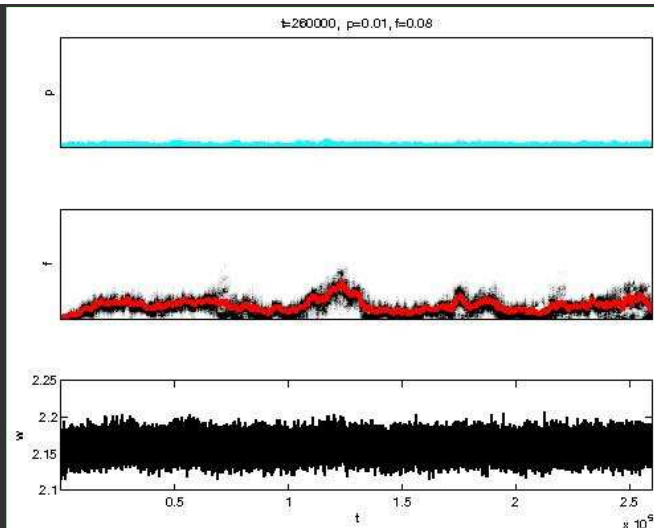
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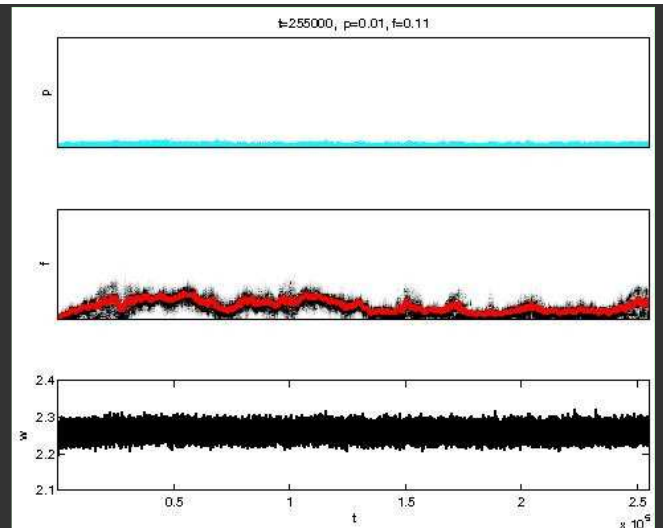
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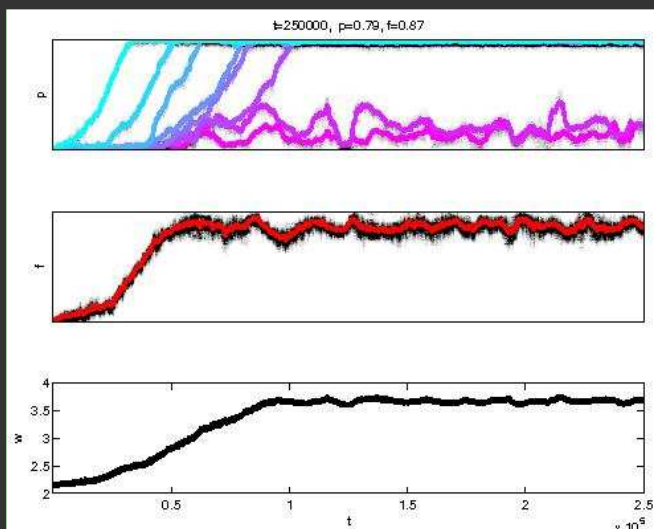
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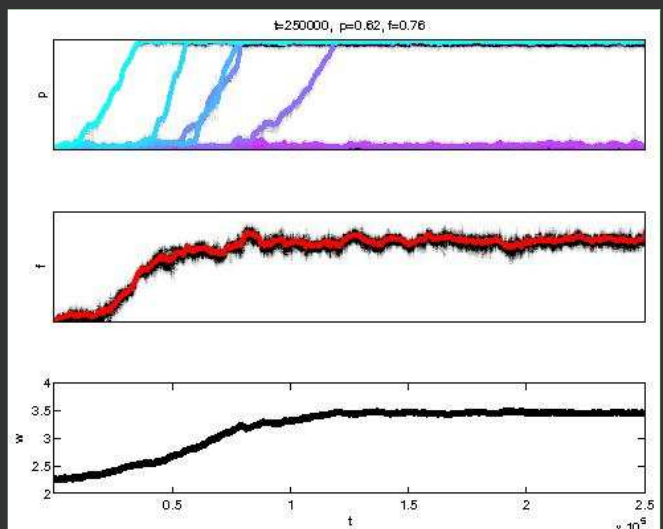
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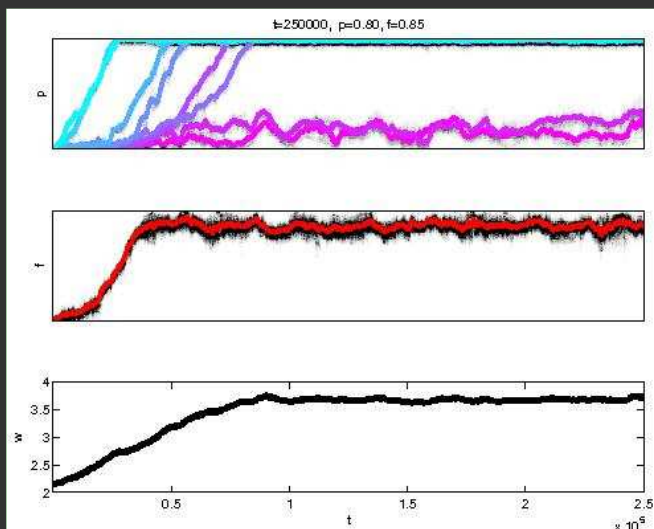
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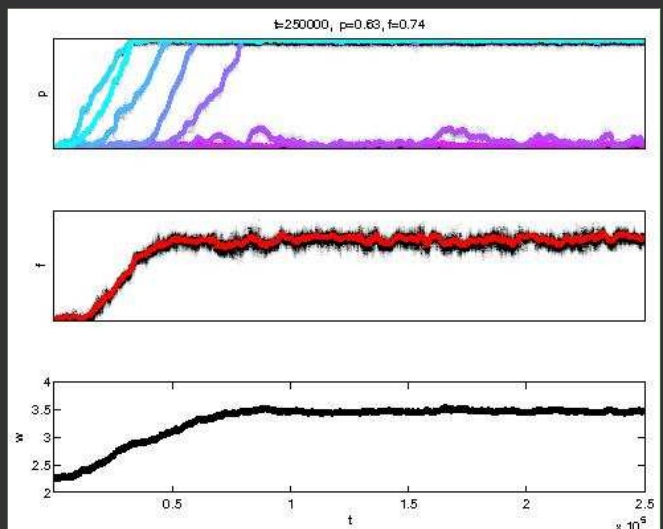
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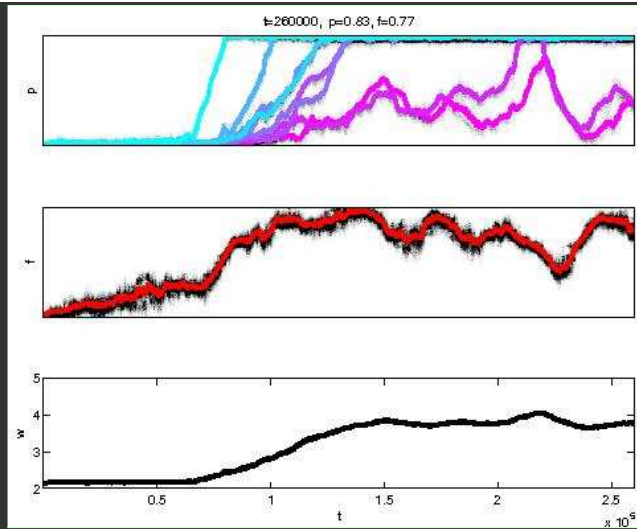
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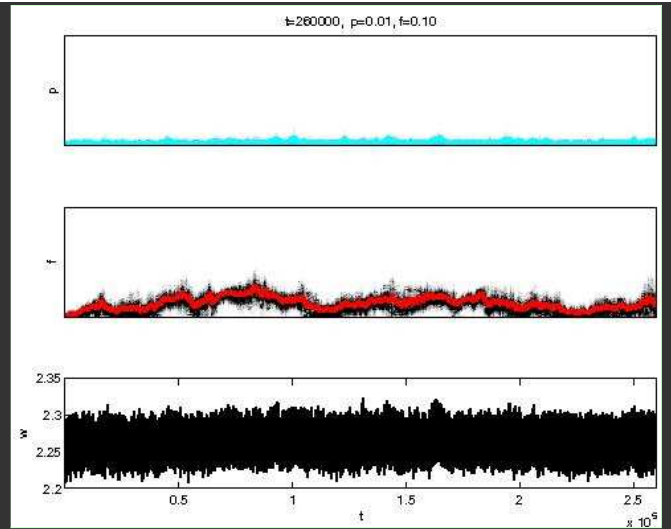
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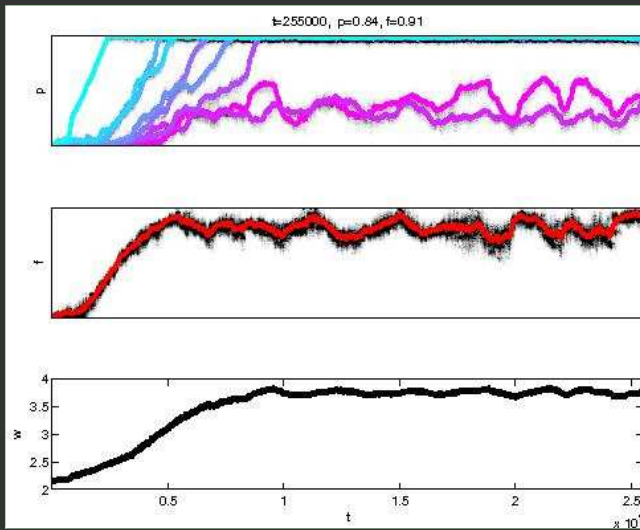
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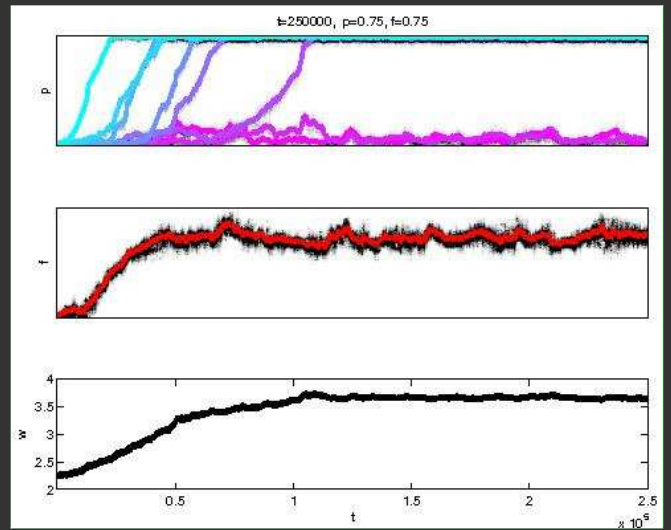
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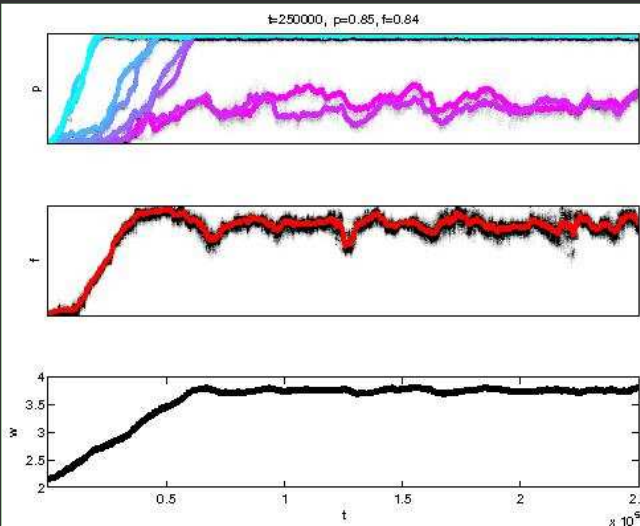
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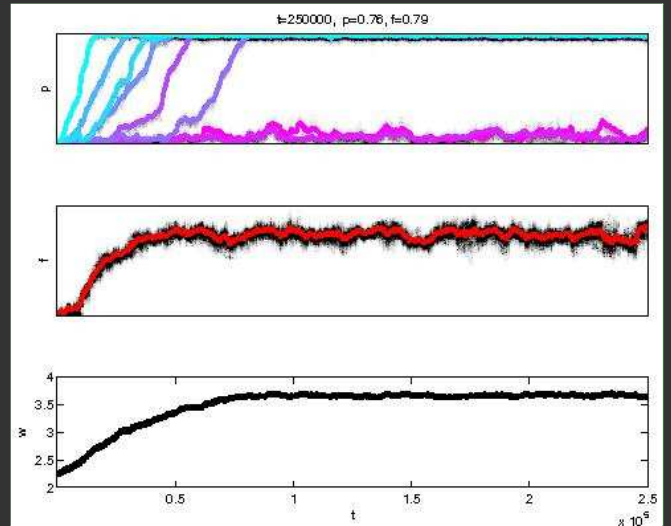
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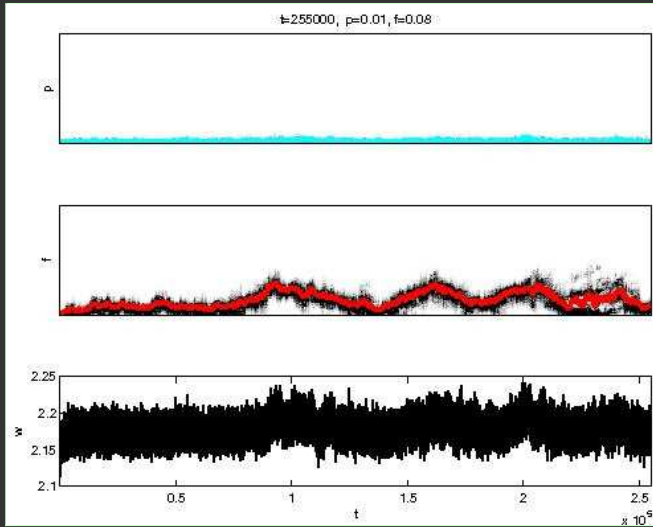
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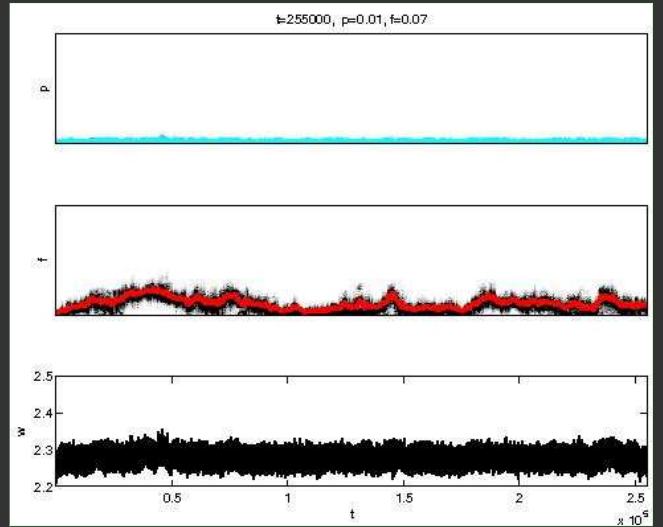
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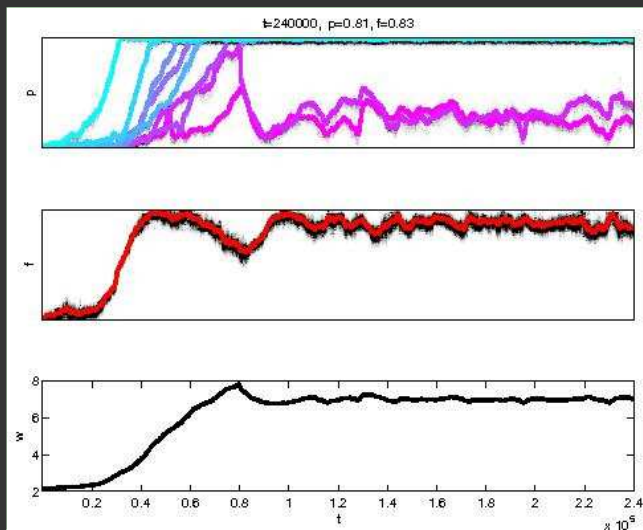
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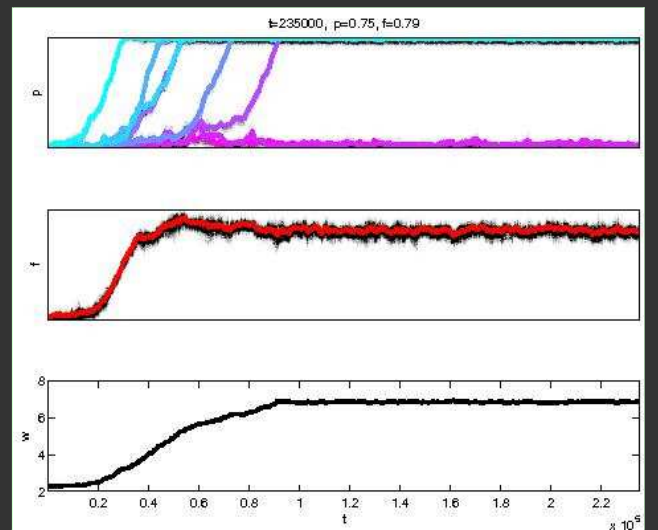
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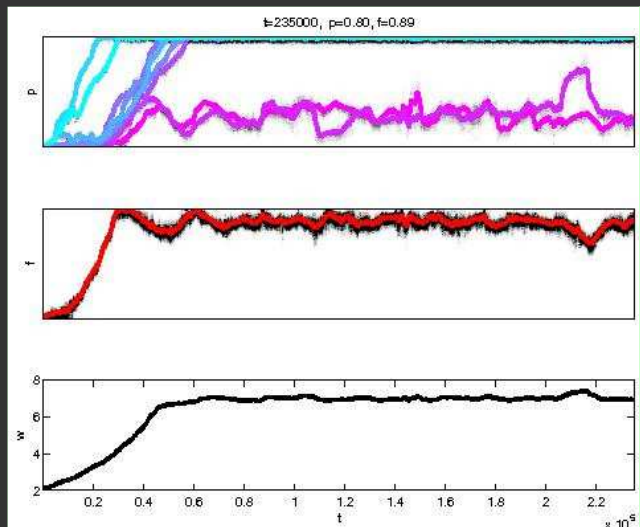
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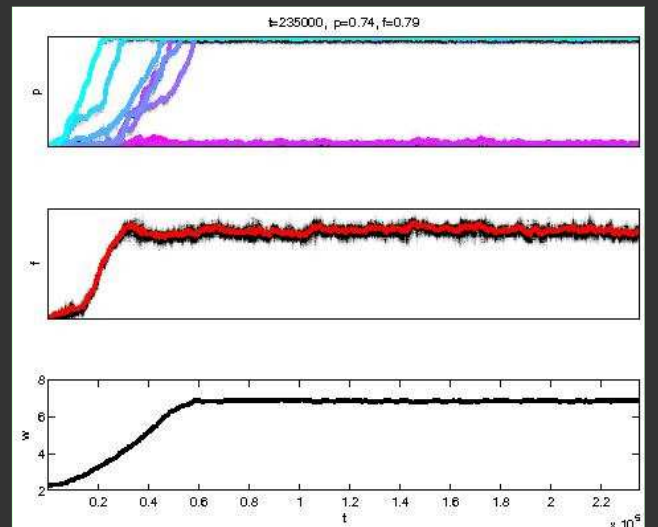
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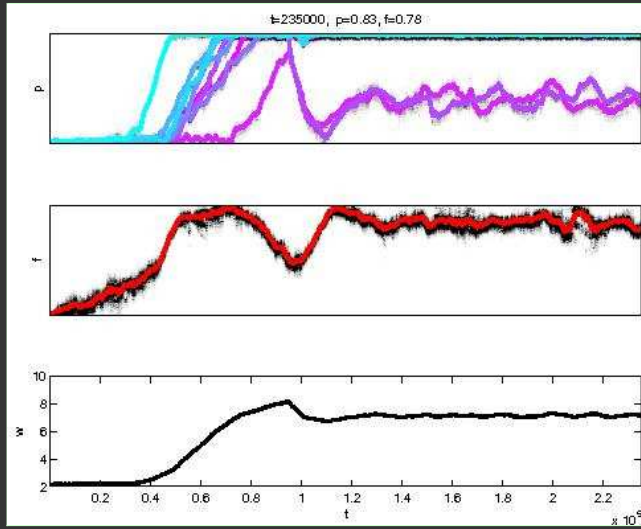
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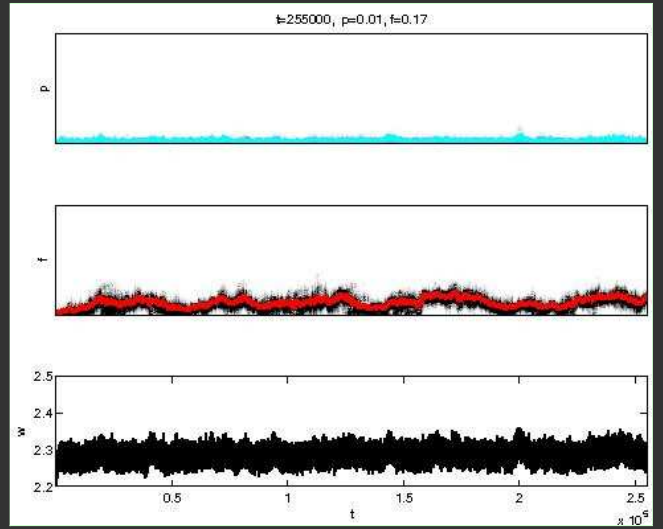
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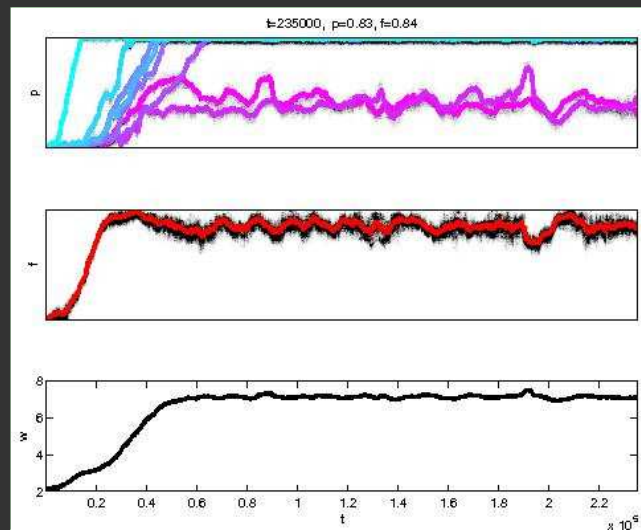
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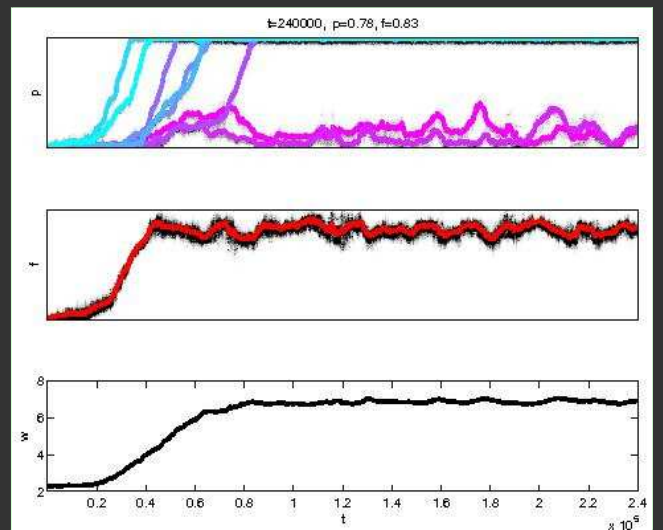
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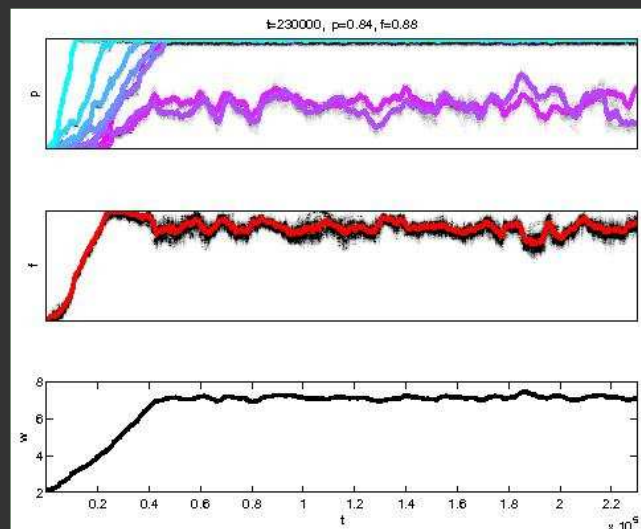
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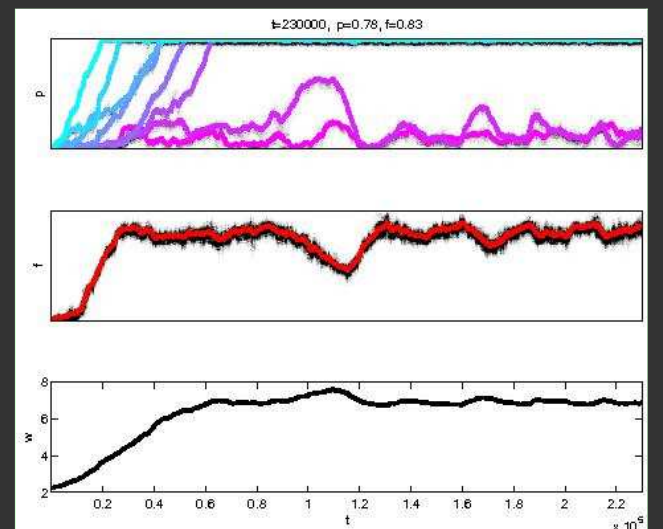
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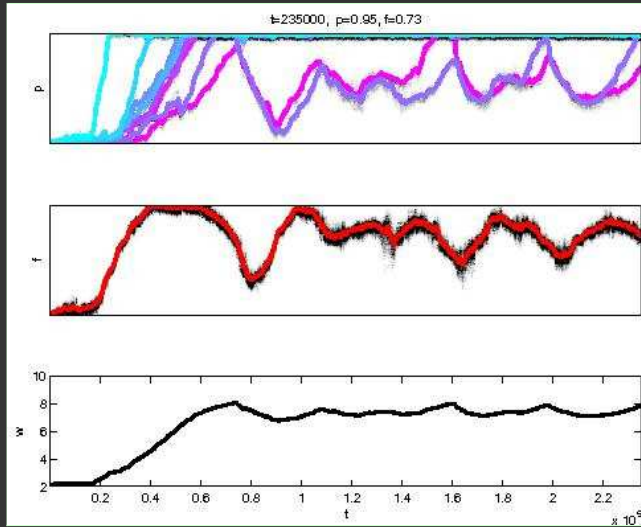
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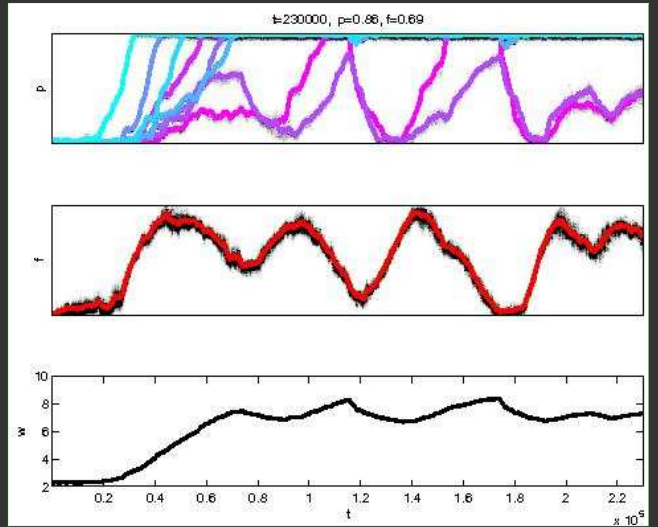
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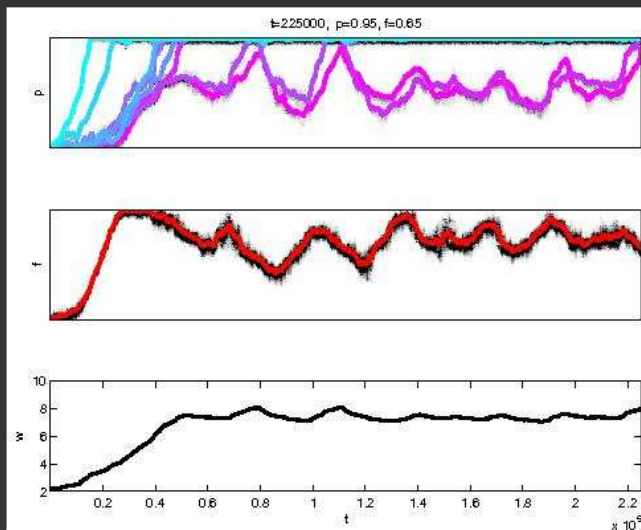
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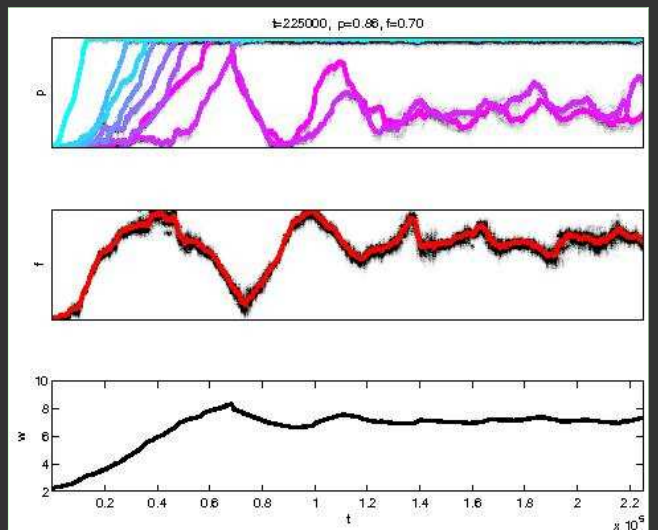
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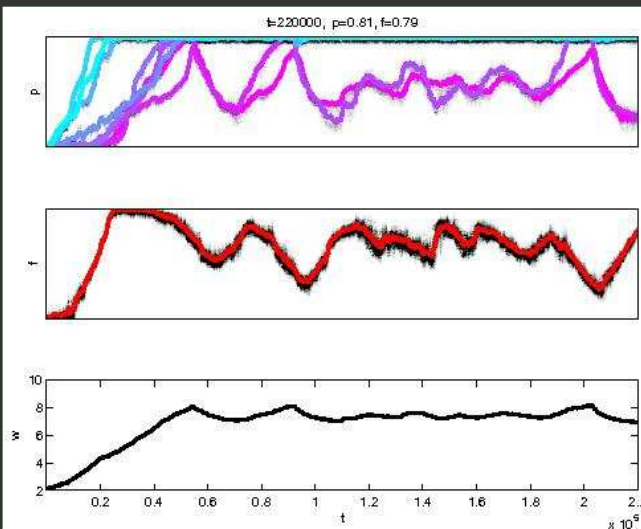
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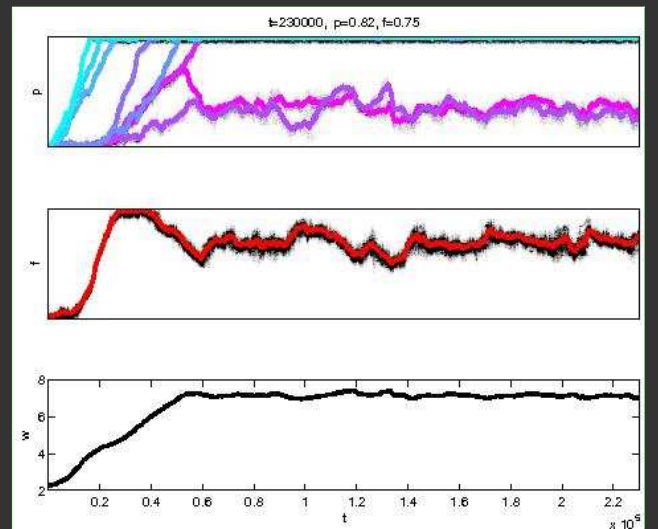
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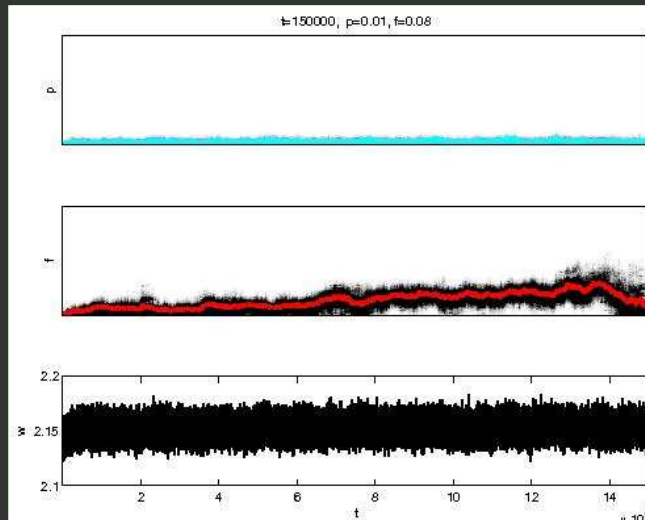


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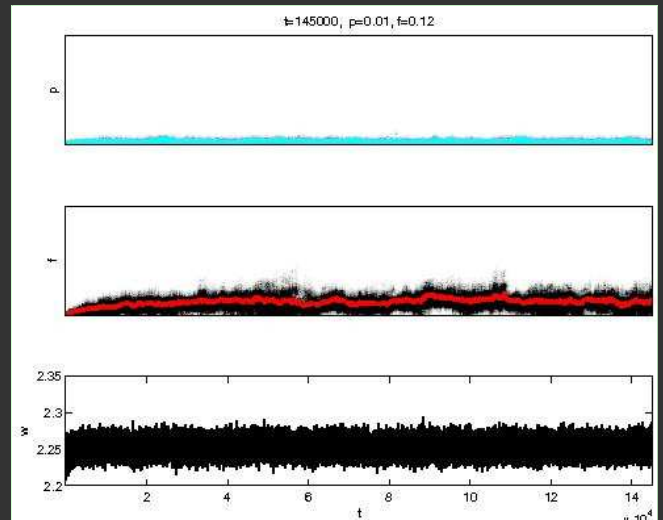
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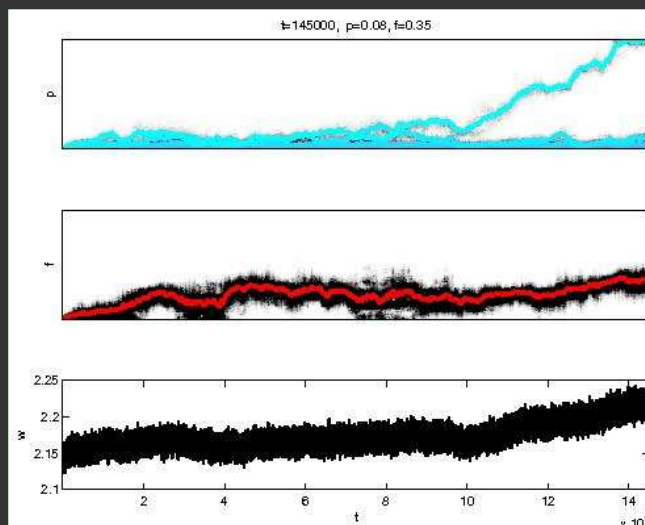
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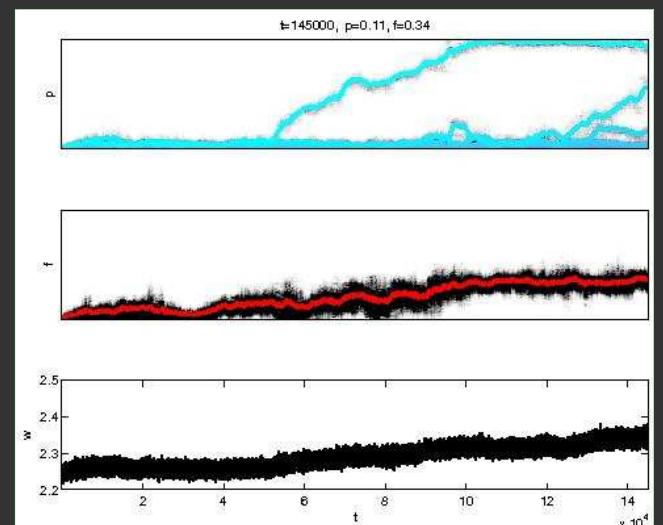
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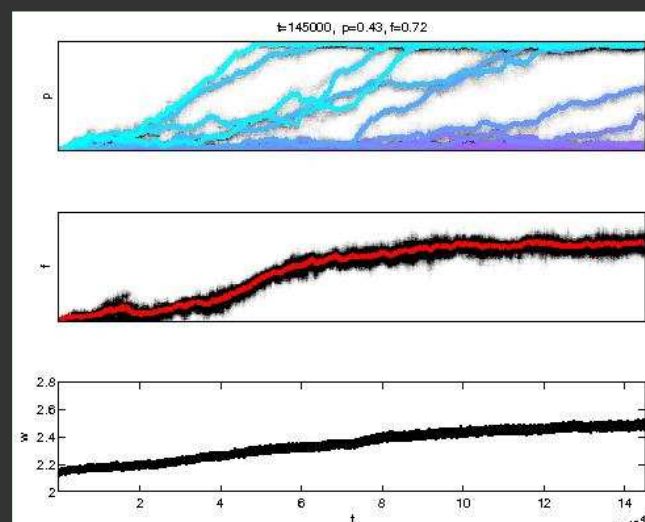
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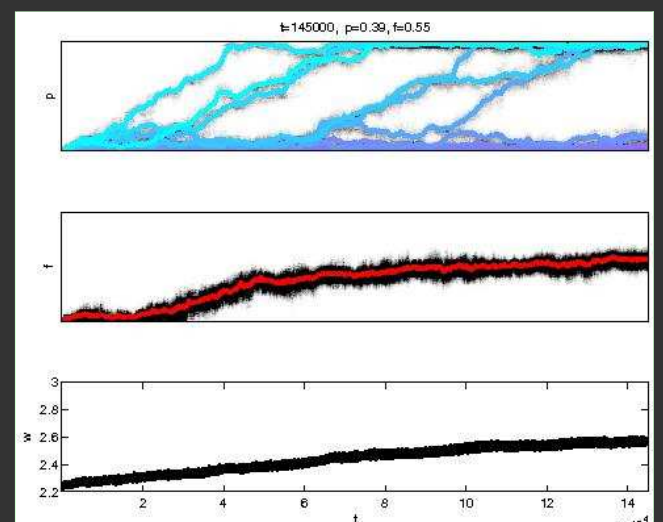
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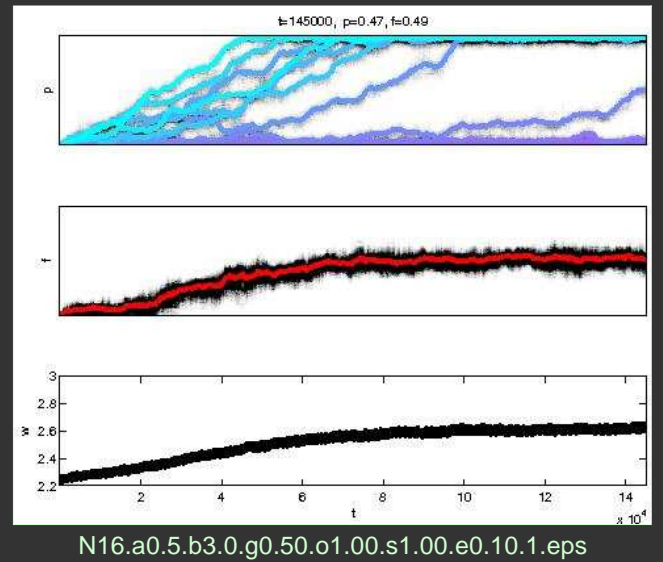
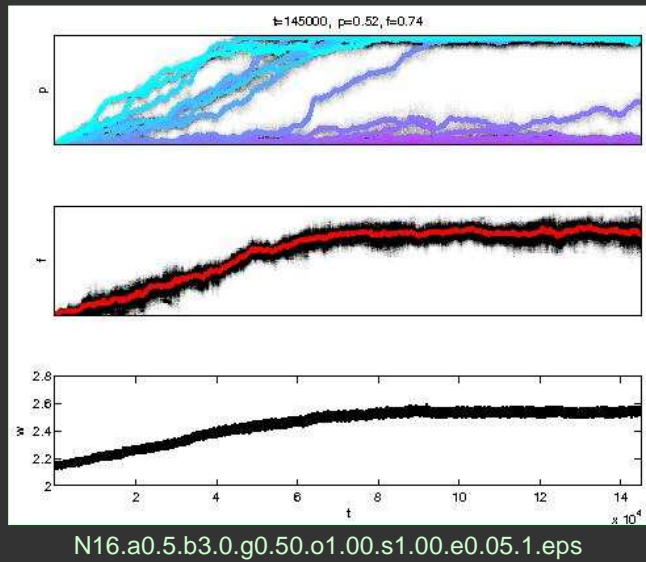
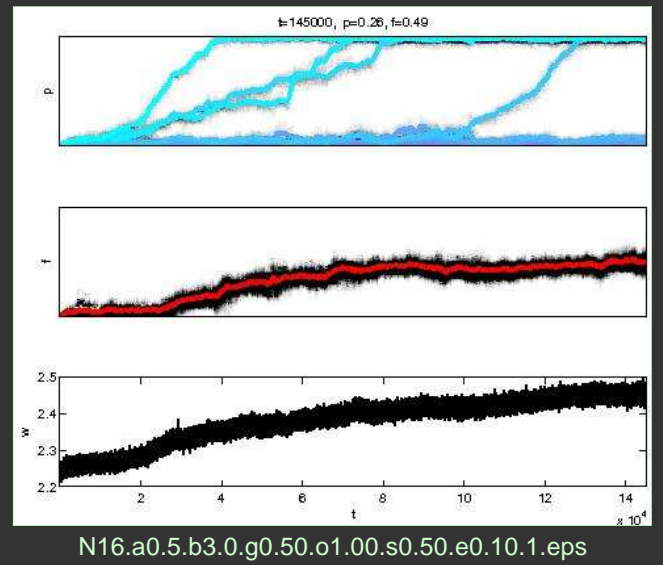
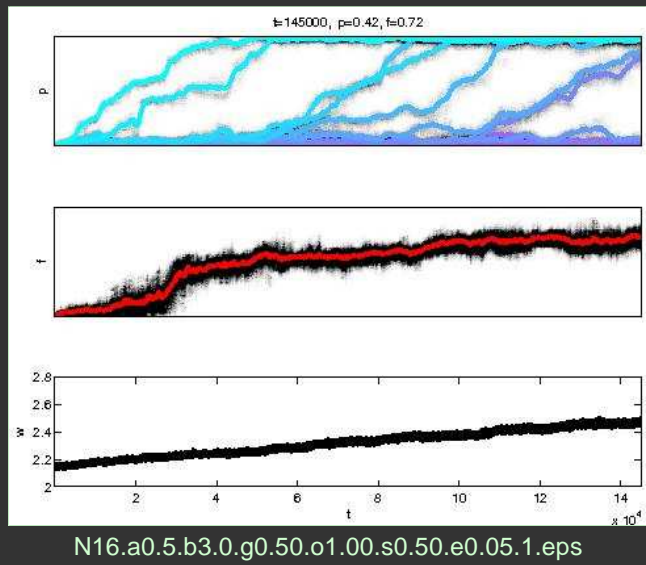
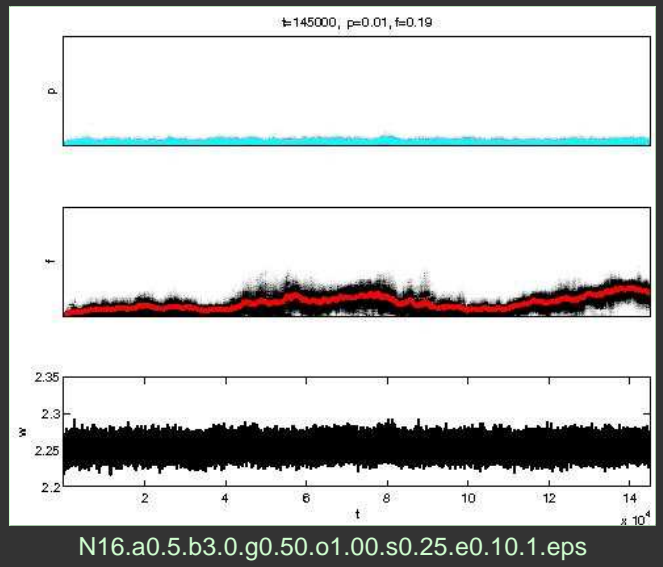
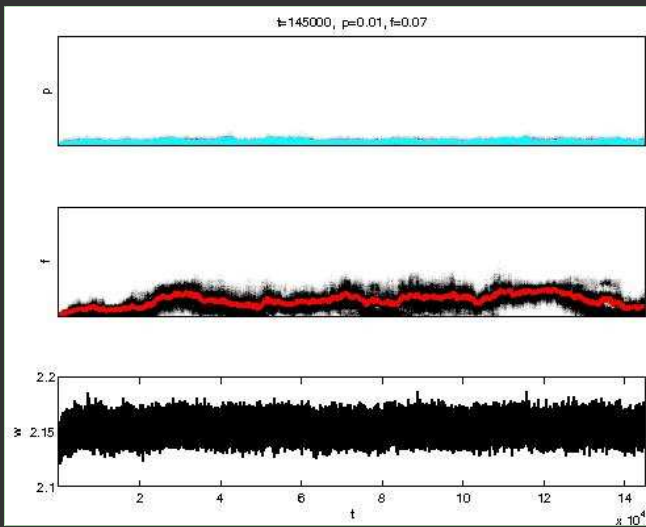
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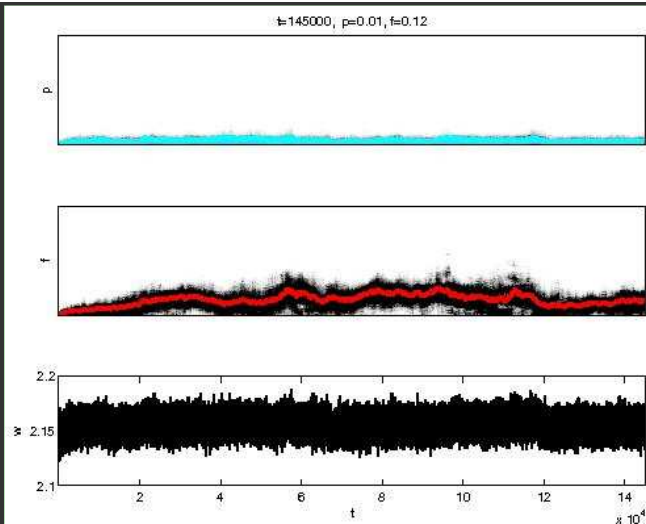


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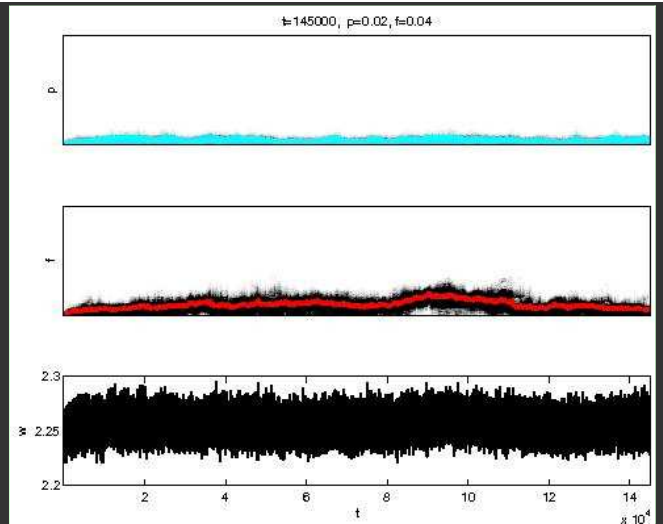


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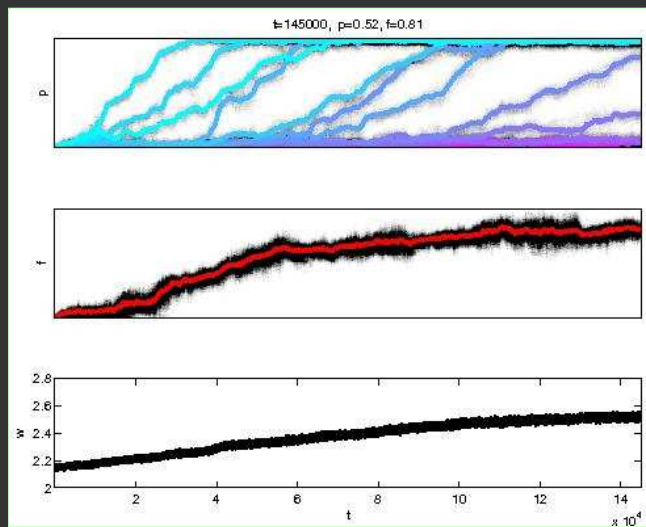




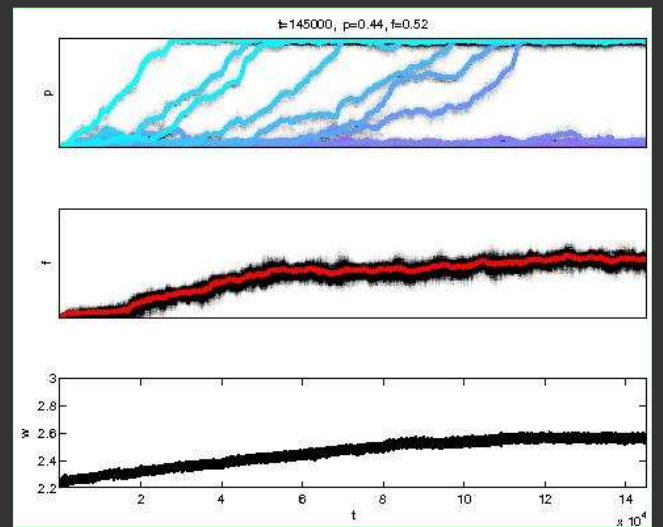
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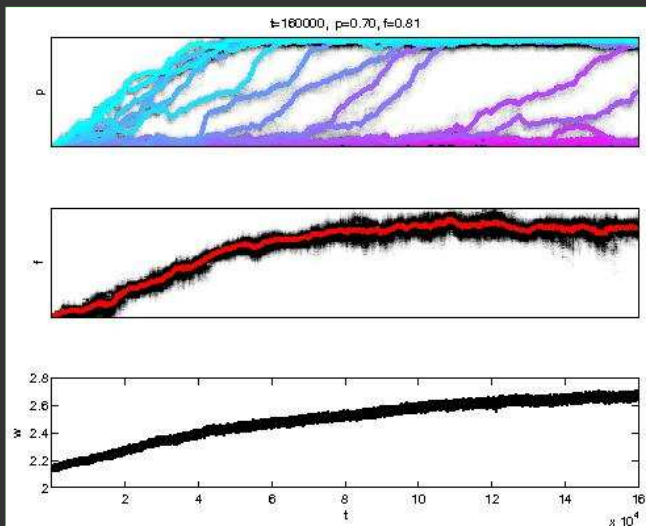
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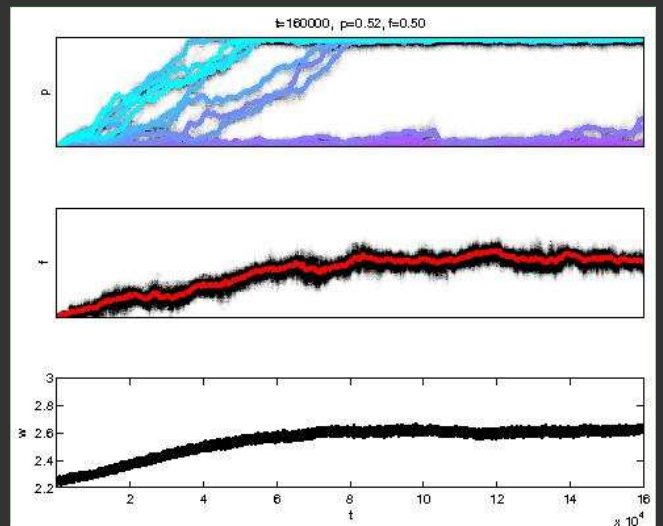
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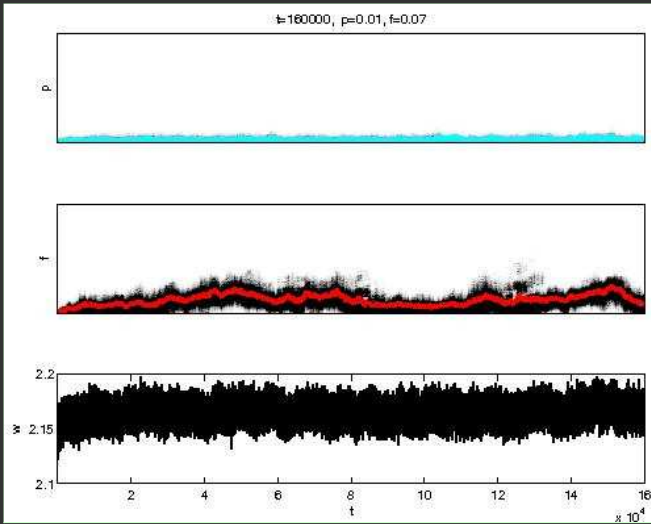
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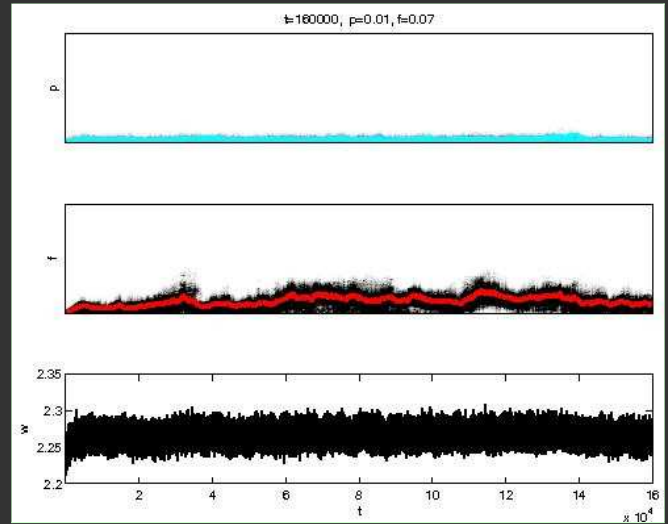
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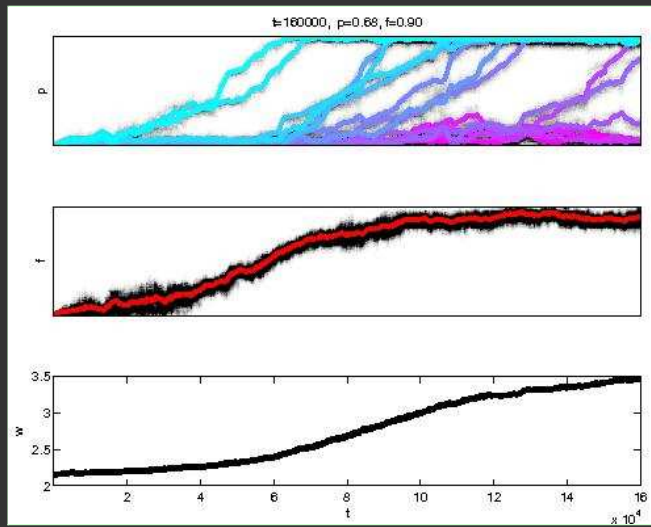
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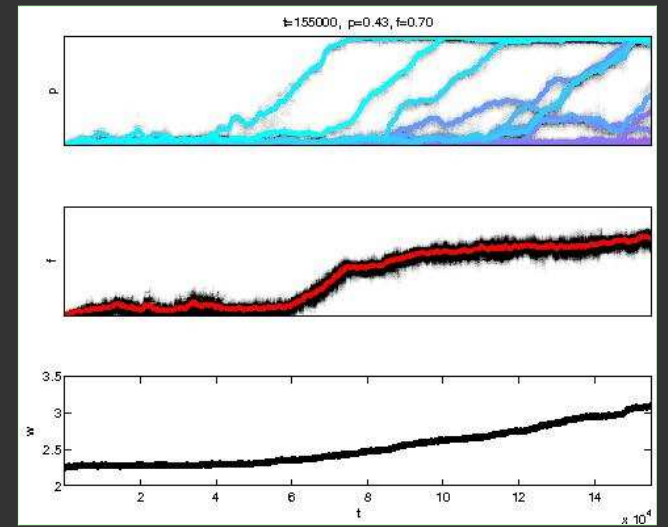
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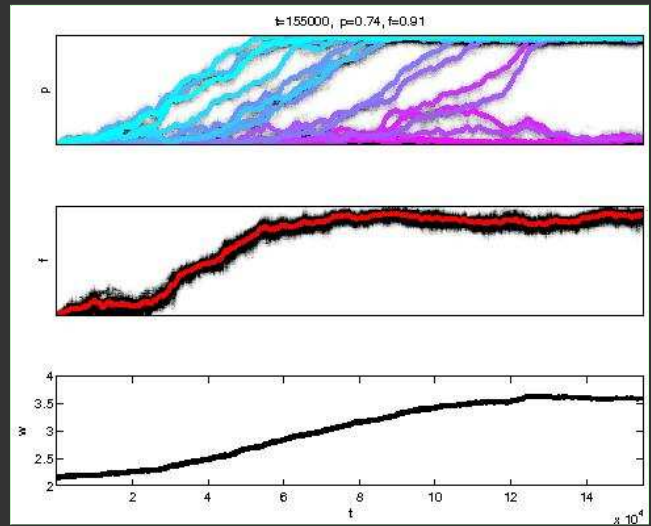
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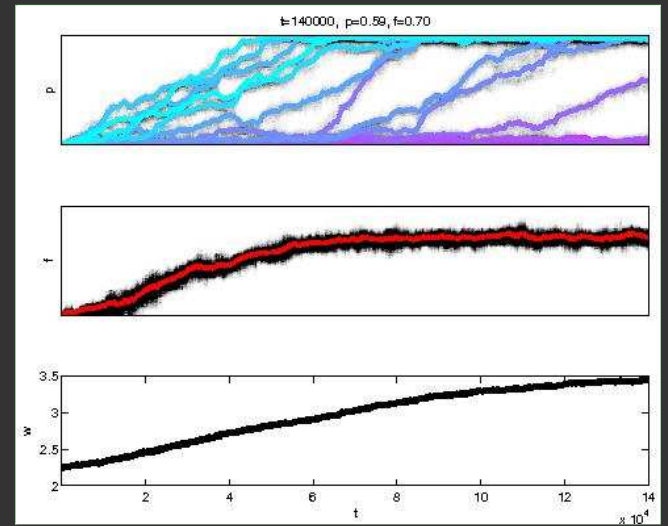
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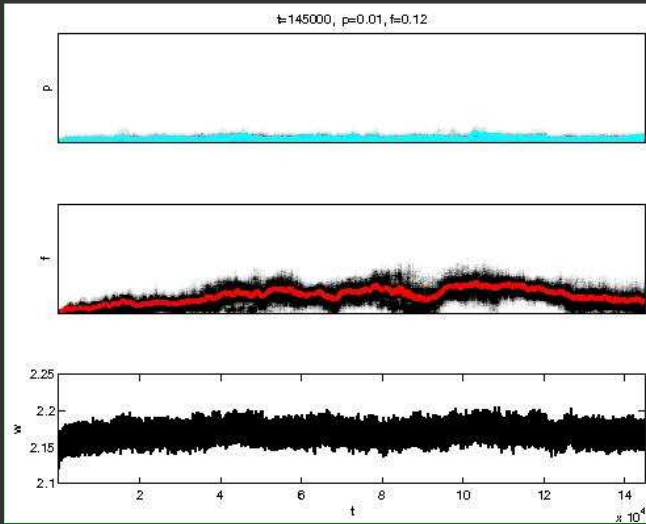
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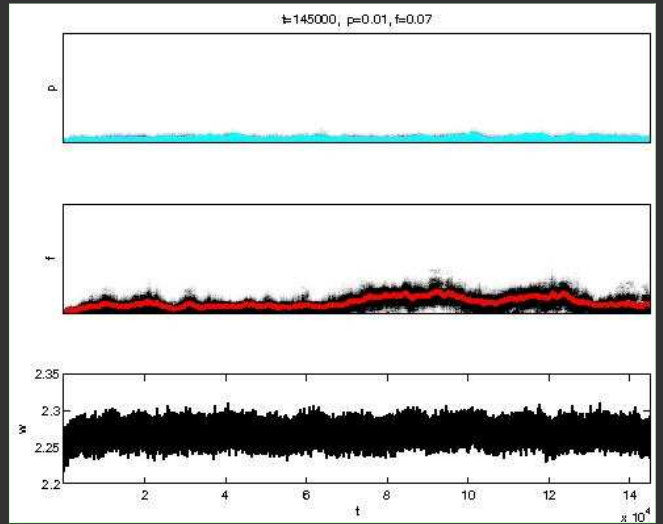
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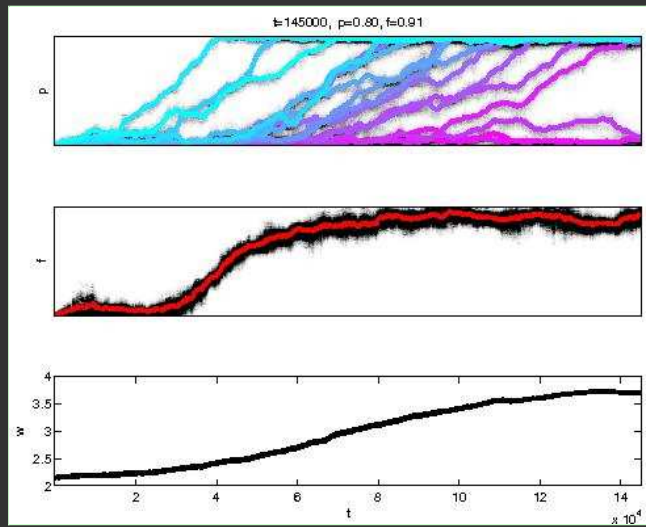
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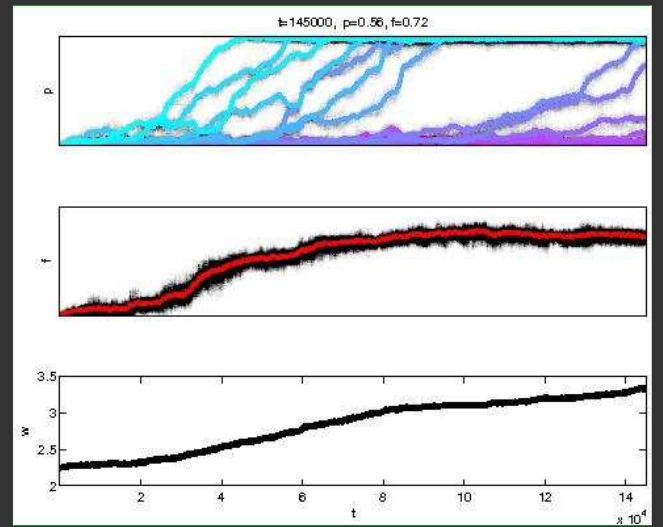
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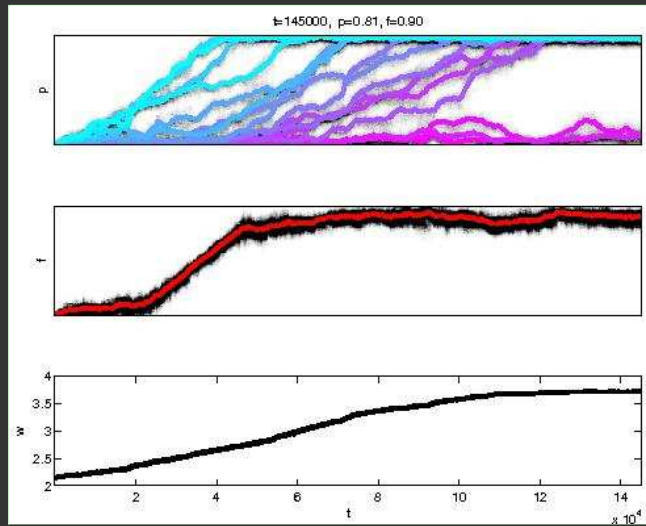
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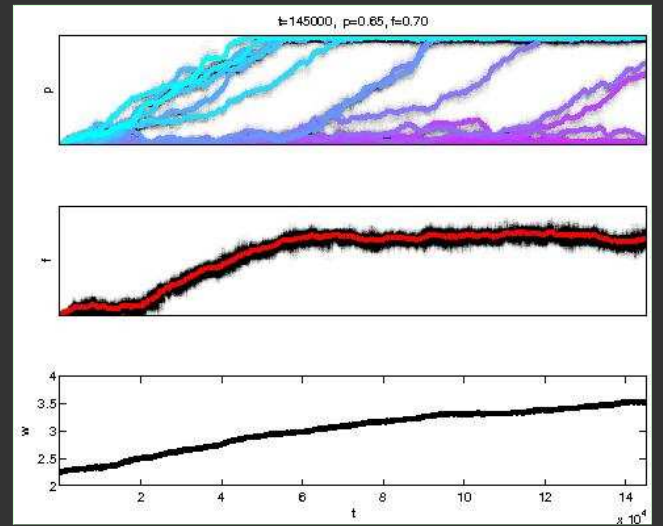
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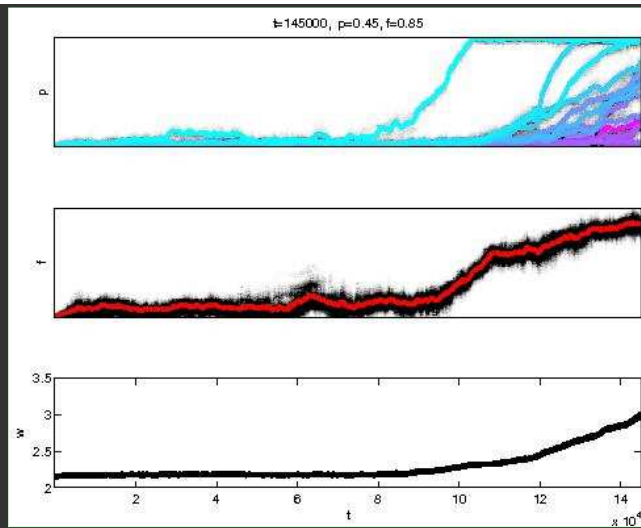
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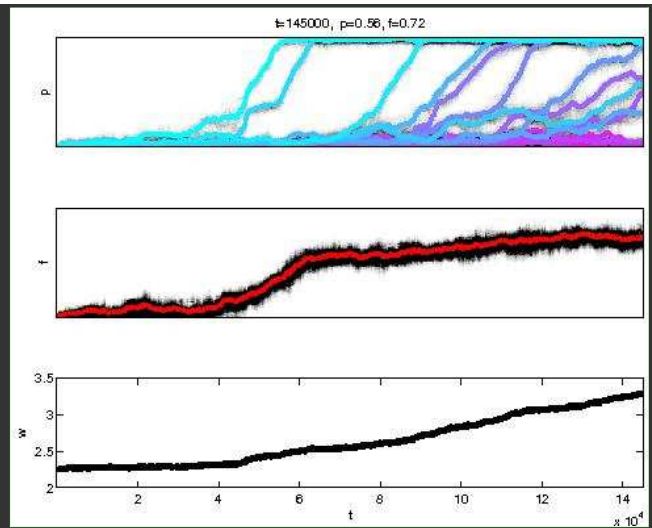
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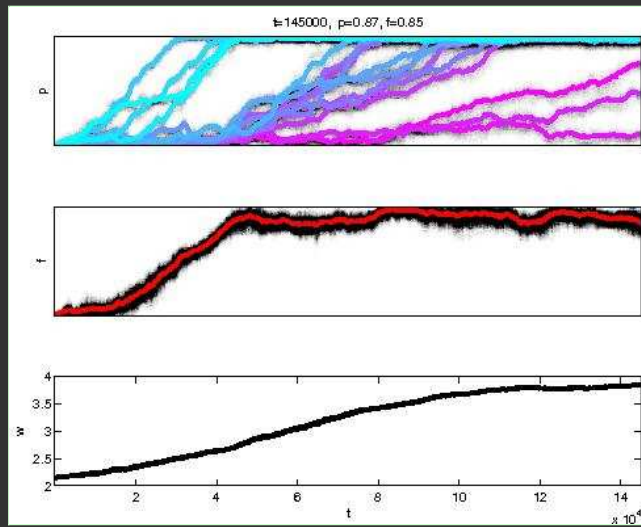
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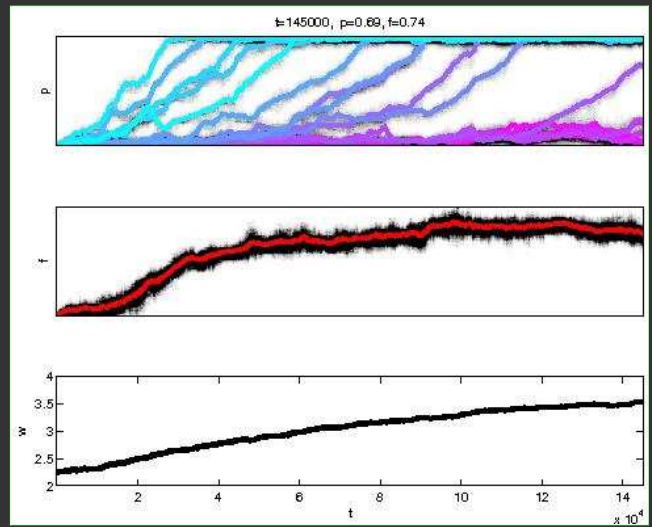
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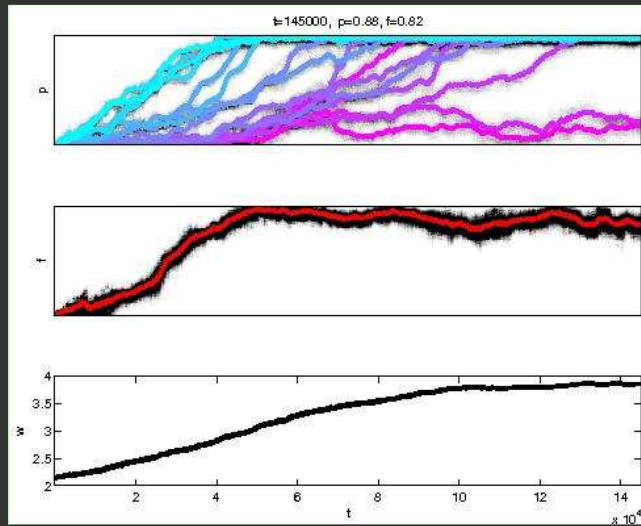
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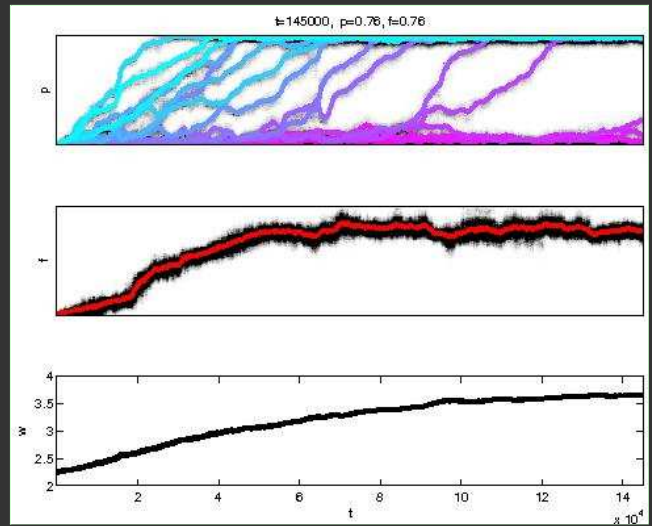
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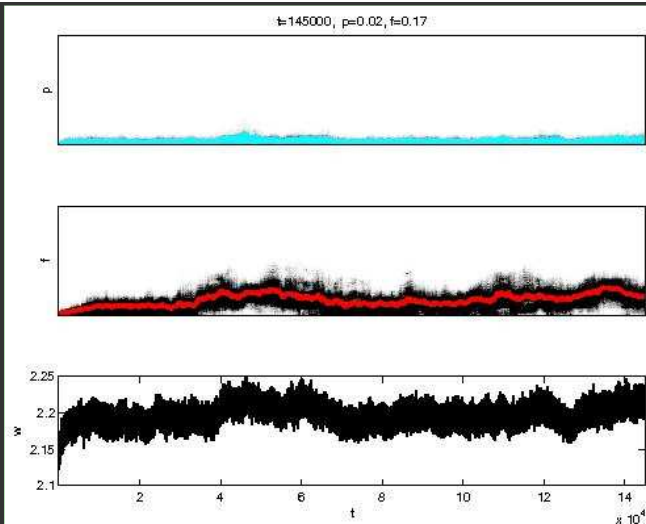
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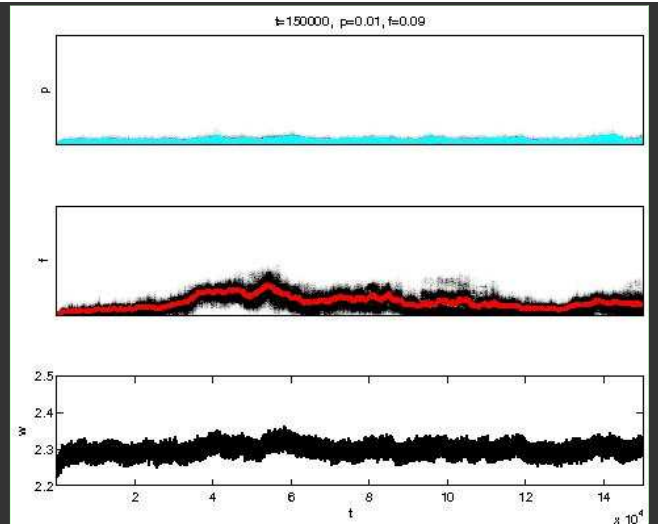
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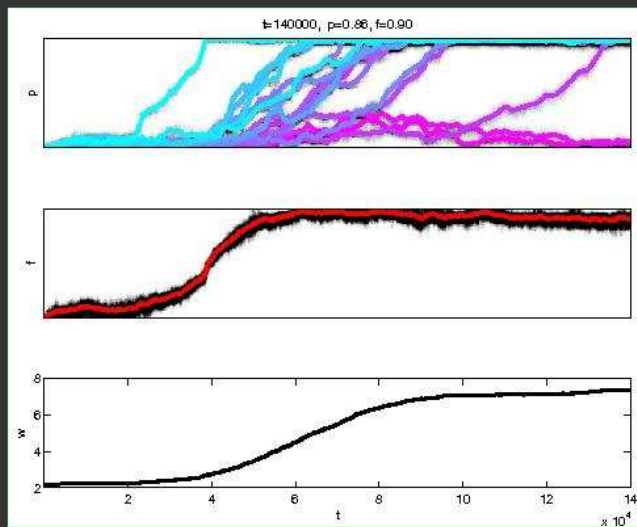
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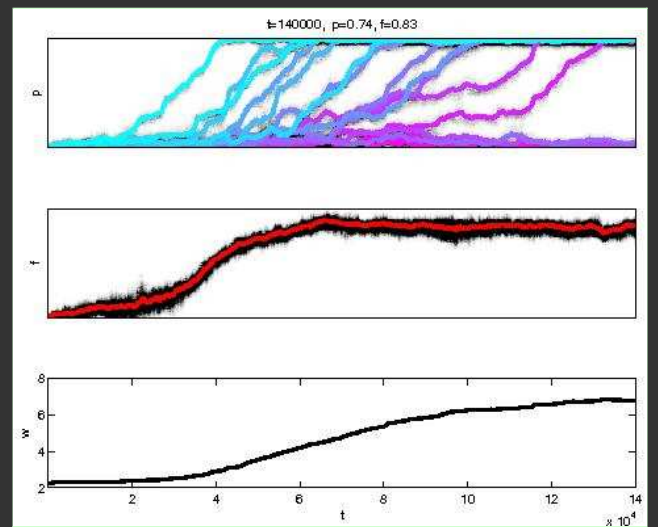
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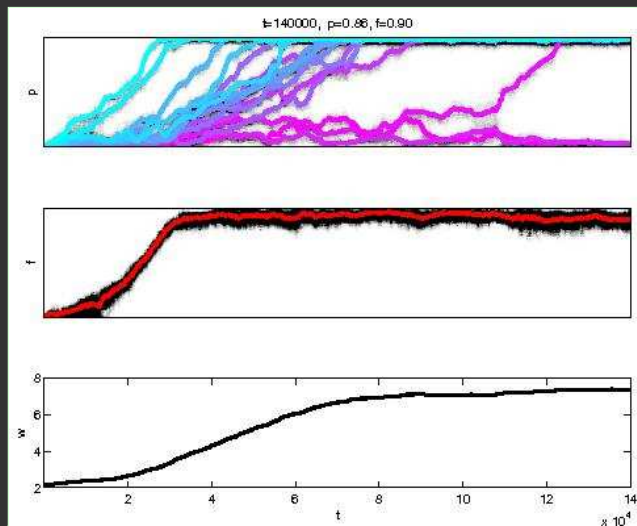
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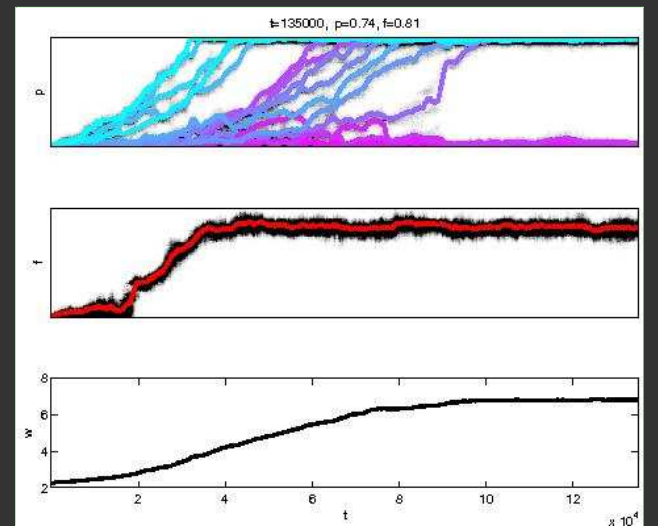
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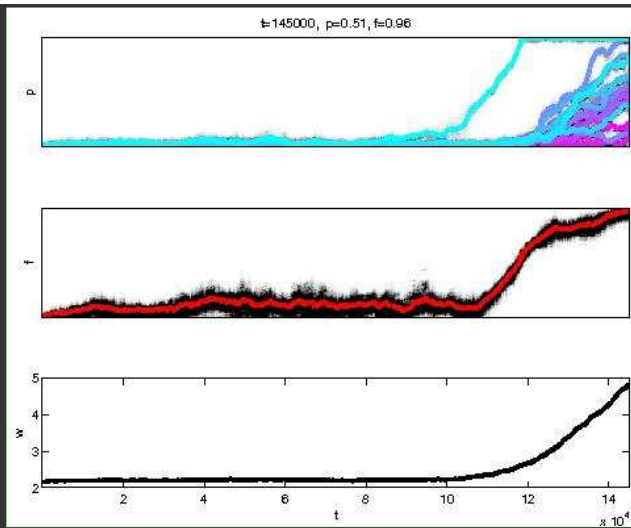
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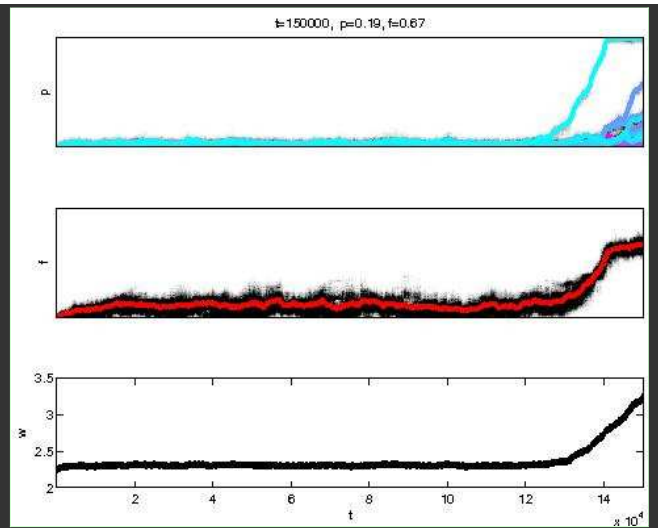
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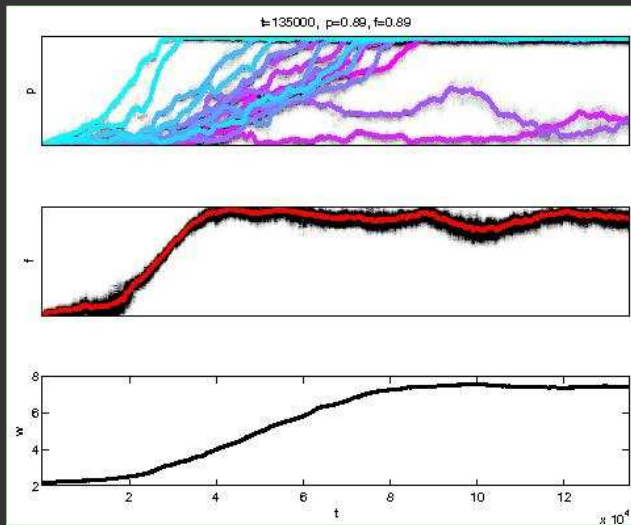
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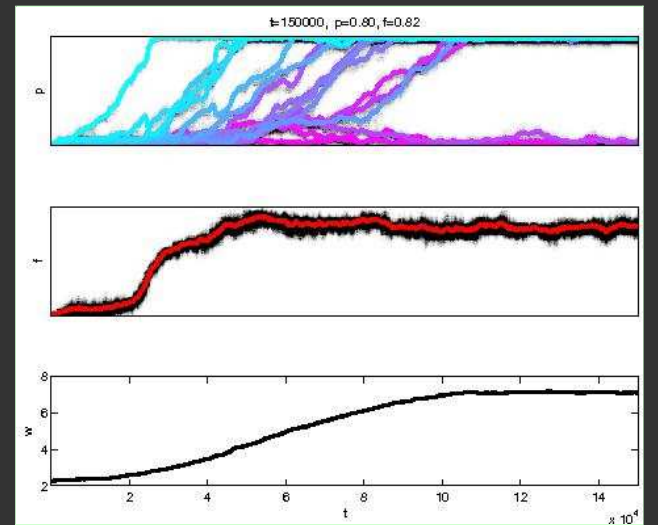
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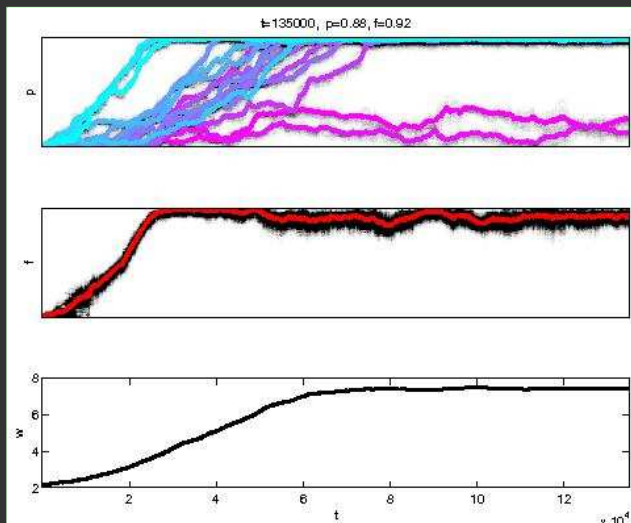
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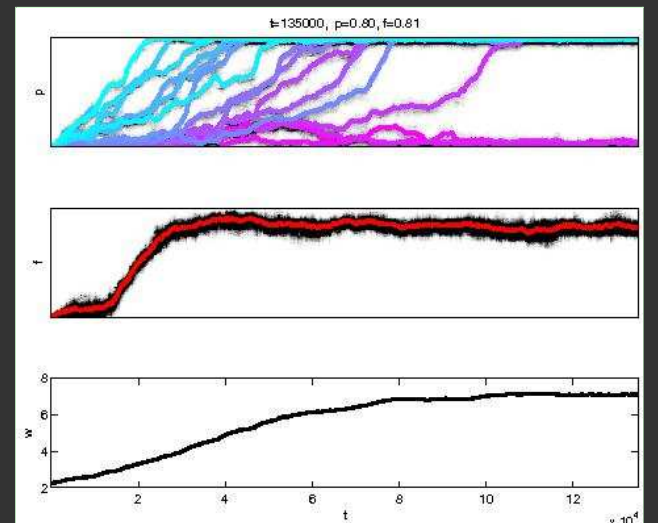
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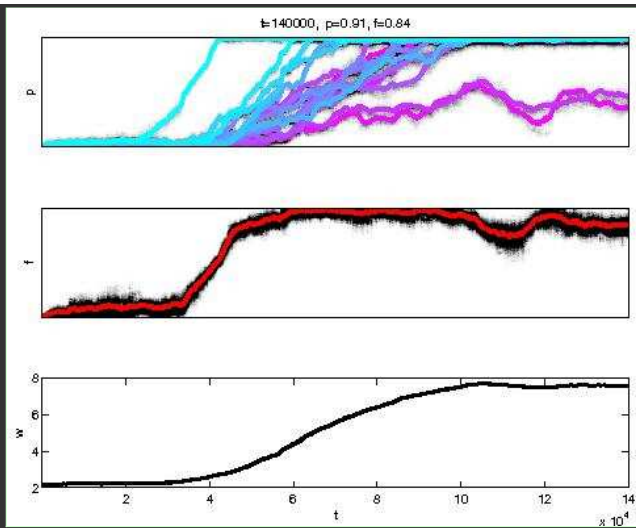
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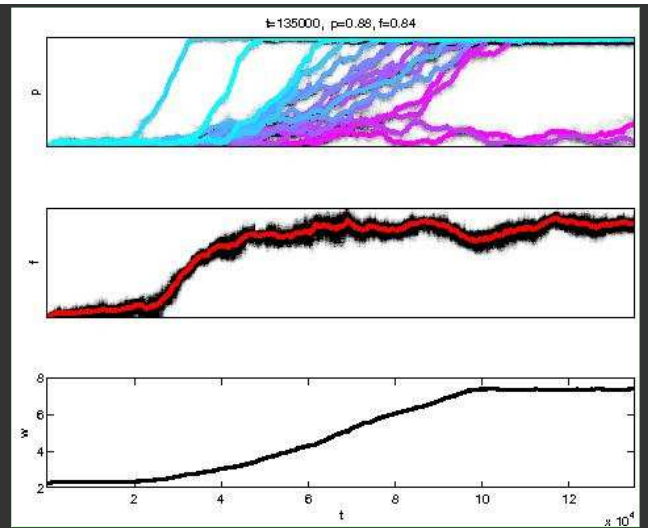
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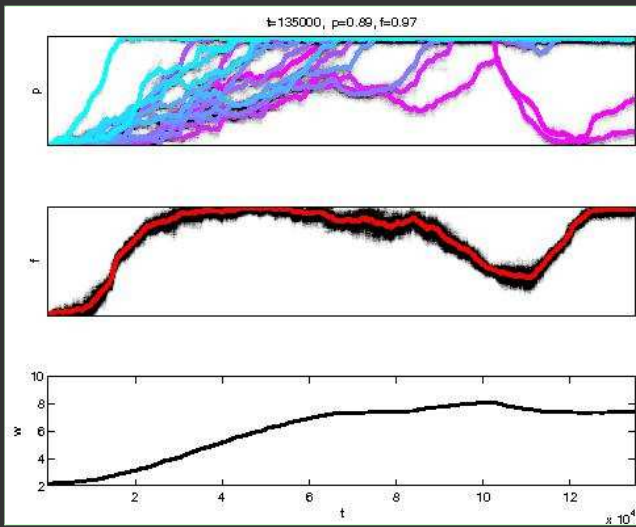
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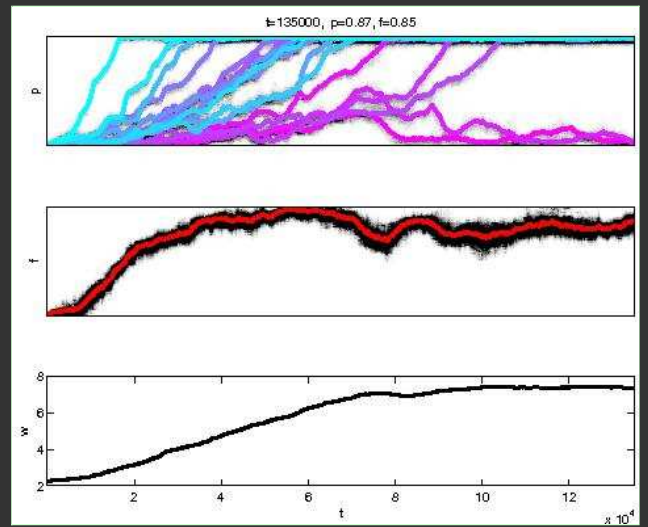
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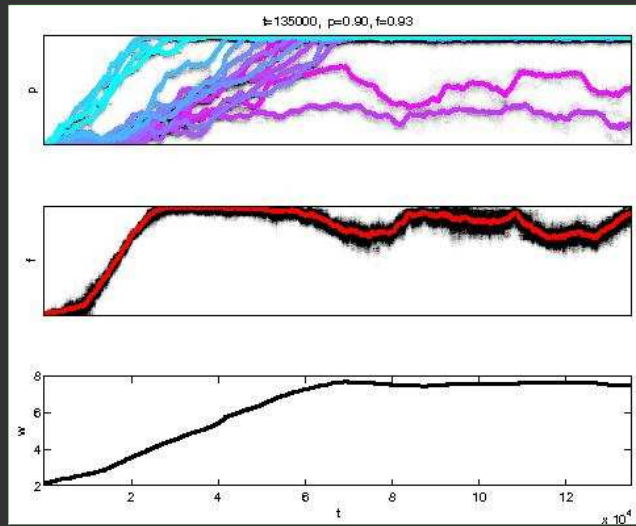
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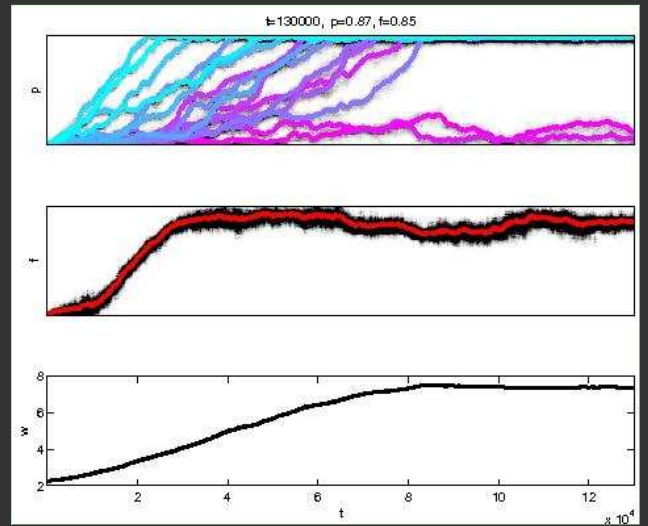
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