

# Death-birth ordering and suppression of fitness in networks

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## Abstract

We investigate how easy it is for fitter variants in a population to invade a network that consists of a “hub” connected to many “spokes”. Birth-death processes are known to amplify the effects of fitness over neutral drift in such a network (as well as in more complex ones such as scale-free graphs). Death-birth processes are identical in all respects except that deaths cause births at neighbouring sites. We show that death-birth processes lead to fitness being strongly suppressed and almost eliminated as an evolutionary force in the hub-and-spokes network. This clarifies which of the two dynamical models is appropriate in a given scenario: under birth-first dynamics links represent risks, whereas in death-first dynamics they are opportunities.

*Key words:* Fixation probability, Moran process, evolutionary graph theory, neutral evolution, birth-death process

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## 1. Introduction

Evolution proceeds via the spread of successive inherited changes throughout a population. If most individuals have similar fitness but one carries a fitness-enhancing mutation, the mutant strain may spread and eventually take over the whole population, or it may simply die out through bad luck. Accordingly there is interest in whether fitness-driven versus neutral (12; 2; 13; 14) evolutionary tendencies are likely to dominate in different scenarios (18; 21). Here we consider populations that are structured as a network, with individuals inhabiting the nodes, and links determining which nodes interact with one another. A natural question is how likely a lone mutant is to eventually take over all the nodes in such a network. This probability depends strongly on the graph structure, but as we will show it also depends critically on the way that individuals are allowed to invade one another.

### 1.1. The Moran process and amplification of fitness

The Moran process (17; 18; 20) on a graph (15; 21; 28) is a simple way to model invasions. In the simplest case each individual has an intrinsic fitness that determines its reproductive output. Each step of the dynamics consists of

(i) choosing a birth site with probability proportional to the fitness of its occupant, (ii) choosing a death site at random from the neighbours of the birth site, and (iii) replacing the occupant of the death site by a copy of the one at the birth site. The more complicated case of neighbour-dependent fitness (“games” modelling cooperation for example) has also been studied (22; 23; 1; 10; 11; 29) but here we look at the model in its most basic form.

Suppose the network is initially populated by individuals of fitness 1. The fixation probability  $\rho(r)$  is the chance that a lone mutant of fitness  $r$ , started from a random node, eventually takes over the whole population. For a fully connected network this probability is (19):

$$\rho(r) = \frac{1 - 1/r}{1 - 1/r^N} \quad (1)$$

where  $N$  is the number of nodes. The same equation can be shown to hold for any network in which all nodes have the same number of links (as well as to classes of the more general form in which links are given relative weightings). Although it is not immediately obvious,  $\rho \rightarrow \frac{1}{N}$  as  $r \rightarrow 1$ , as is clear from symmetry.

For example consider a population of 100 individuals. A mutant with “neutral” ( $r = 1$ ) fitness has a 1 percent chance of taking over, but for a mutant with fitness 2 this jumps to just over 50%. If the enhanced fitness only lasted for one generation then an  $r = 2$  individual would in a sense be equivalent to two identical  $r = 1$  mutants and have the same chance of reaching fixation, namely  $2/N$ . But because fitness is taken to be inherited, the fixation

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probability “blows up” and becomes almost independent of  $N$ . So even though this mutant initially appears as one of a very large crowd, it has a good chance of taking over regardless of how big the crowd is.

Interestingly, despite spatial structures being irrelevant to evolution in many cases (16; 25), under the Moran process certain graph structures have the effect of raising  $\rho(r)$  even more than this (15). For example in a star-shaped network consisting of a hub and spokes the fixation probability is given by equation 1 but with  $r$  replaced by  $r^2$ . Under the Moran process the STAR network is, in effect, an amplifier of fitness. Other graphs have been shown to be even more powerful amplifiers, but the STAR is the most plausible, and simplest, that shows the effect.

The usual Moran process on a graph puts birth “before” death, in that deaths are chosen from the neighbours of the birth site. In this paper we compare this with what happens if we instead assume that death occurs “first”, and the birth is then chosen from its neighbours. Surprisingly, this minor change leads to strong *suppression* of fitness on the hub-and-spokes graph - the same network that amplifies it under the Moran process.

## 1.2. Four simple update rules

We denote the Moran dynamics as a *birth-death* (B-D) process, since births lead to deaths at neighbouring sites. An alternative ordering is a *death-birth* (D-B) process in which deaths lead to contingent births at neighbouring sites. This is sometimes called a Voter model (9; 8; 7; 5). For example, at every update we could first choose a site at random to be the location of a death, and then choose one of its neighbours (with probability proportional to fitness) to provide the replacement via birth.

In both of these cases fitness enters the update rule via the choice of birth site, whereas the choice of death site is “neutral”, *i.e.* uniformly distributed amongst the available options. Adding a lowercase  $f$  to make explicit the role of fitness, we use Bf-D and D-Bf to refer to this form of the Moran and Voter processes respectively. Higher fitness implies a higher probability of being “chosen” for birth, which seems a non-controversial position to take. However one might plausibly argue that fitness should bias the choice of death site. To model this we can have births occur at randomly chosen sites and deaths be chosen from neighbours of the birth site with probabilities proportional to their ‘unfitness’, this being some decreasing function of fitness  $f$ . We denote this process B-Df. This immediately suggests a fourth variant, in which a death is chosen globally but with probability proportional to unfitness, and the birth site is chosen at random from among its neighbours. This Df-B process is also known as the biased voter model (e.g. in (26; 3), where  $u = 1/f$ ).

We thus have four possible Moran-like dynamics. Some may reflect reality better in particular systems or circumstances than others. One goal of this paper is to clarify

what those circumstances might be.

## 2. Fixation probabilities under these dynamics

We measured  $\rho(r)$  via simulations and calculated it exactly, to compare the four dynamics occurring on fully connected and STAR networks. For simulations the network is initialised with a mutant at a random site and the dynamics continued until fixation by either the “null” occupants with fitness 1 or the mutants with fitness  $r$ . This is carried out many times and we record the ratio of those that led to fixation by the mutant. Alternatively one can note that this is a Markov process and construct a matrix of the transition probabilities between states. The symmetry in each of the two architectures means we only have to keep track of transitions between a few states. In the FULL network there are  $N + 1$  relevant states, corresponding to the number of mutants present (0 to  $N$  inclusive). In the STAR case there are  $2N$  states, corresponding to a number (0 to  $N - 1$ ) of ‘spoke’ nodes containing mutants in the case that the ‘hub’ is, or is not, a mutant. Raising this matrix to a high enough power yields the long term transition probabilities from any initial state to the two absorbing states, so we can read off the fixation probability for the case of one initial mutant transiting to all  $N$  sites being occupied by mutants. In the case of the STAR one takes an appropriately weighted sum of the fixation probabilities for the two possible initial positions (hub and spoke) of the mutant. An advantage of the exact calculation is that it scales up easily to large networks, whereas the simulation becomes slow. A disadvantage is that for networks without such strong symmetries to exploit the exact calculation becomes more complex.

Figure 1 shows results of the exact calculation for the 4 dynamical models and as a function of the number of nodes. We made unfitness inversely proportional to fitness:  $u(f) = 1/f$ . In all cases we used  $r = 2$ : the mutant is twice as fit as the rest.

For fully connected graphs all four dynamics give very similar results as  $N$  grows, namely the fixation probability for  $r = 2$  tends towards 50%. There are slight differences, especially evident for small populations. For example Bf-D and D-Bf are not the same even on a fully connected network, which at first seems surprising. Nevertheless, the probability of an individual being invaded in any one round must be flat ( $1/N$ ) in the death-first case, but in the birth-first one it is lower for high-fitness individuals since deaths are chosen from sites *other than* the birth site. On the other hand the process Df-B *does* follow the Bf-D (Moran) line precisely. Notice that the probability that  $i$  invades  $j$  (called  $p_{ij}$  in Table 1) is  $\propto f_i$  under Bf-D and  $\propto 1/f_j$  under Df-B, so the ratio of the two “fluxes” is the same in both processes, which results ((15) Supplementary Material) in the same fixation probabilities. So the two only match if we use the particular unfitness function  $u \propto 1/f$ . This points to a certain arbitrariness in the choice of this function, which we return to below.

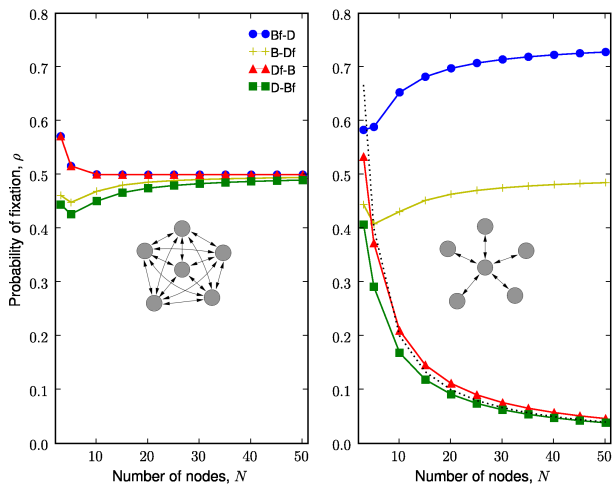


Fig. 1. Exact computations of  $\rho$  for the FULL (*left*) and STAR (*right*) networks, versus the number of nodes  $N$ . The mutant fitness  $r = 2$ . The black dotted line at lower right shows  $r/N$  for comparison.

For the STAR network there are large differences. The most significant is that both of the death-first processes fall away very quickly with  $N$ . Although the mutant takes over slightly more often than a neutral ( $r = 1$ ) one would, overall the scaling of  $\rho$  follows  $1/N$ .

Antal *et al.* (3) analysed Bf-D (Moran) and D-Bf (Voter) dynamics on degree-heterogeneous graphs in general, of which the STAR is a paradigmatic example. Starting with a single mutant at a node of degree  $k$ , the fixation probability is proportional to  $1/k$  for invasion process (Bf-D) dynamics, and to  $k$  for biased voter model (Df-B) dynamics, irrespective of its fitness (which obviously must also affect fixation probability, but in a way that is independent of the starting node's connectivity). It follows that to invade a network in which B-D updating applies it pays to start at a spoke, whereas under D-B updating one should start at a hub. Mutants are assumed to arise at random nodes, which by definition tend to have low  $k$  and therefore to have a decreased chance of fixation.

Note that there is no unique way to define unfitness in terms of fitness - the above simulations happened to use the inverse, but there is nothing automatic about this and we also tried other positive decreasing functions such as  $u = \exp(-f)$ . Different choices shift  $\rho$  up or down (just as redefining fitness to be  $f^2$  would, for example), but qualitatively the trends remain the same:  $\rho$  for D-B goes as  $\sim 1/N$  while for B-D it is large and almost independent of  $N$ . The freedom to choose different unfitness functions makes comparison between the quantitative results for these rules and the others uninteresting. Since the trends are the same, for the rest of the paper we use Bf-D as the birth-first process and D-Bf as the death-first process.

### 2.1. Time taken to reach fixation

The hub-and-spokes network structure also strongly affects evolution in terms of the time taken to reach fixation,

as shown in Fig 2. Under B-D processes fitter mutants reach fixation with a high probability that is almost independent of the system size, although it takes them much longer to do so than it would in the fully connected graph. Under D-B processes fixation is rapid (27) but the mutant's fitness is worth much less: its effect is swamped and evolution should be dominated by random drift.

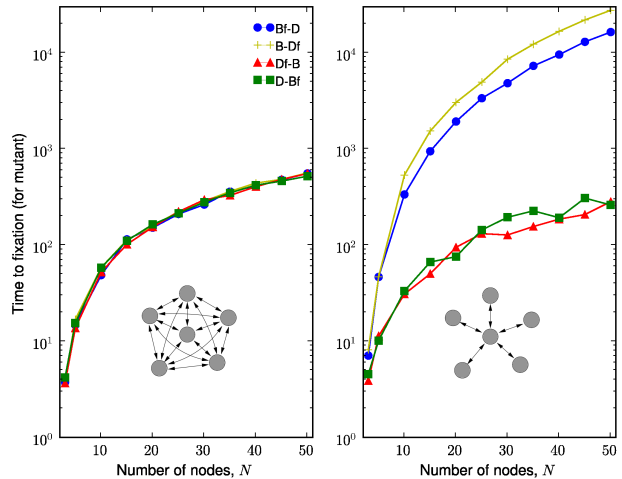


Fig. 2. The time to fixation for the FULL (*left*) and STAR (*right*) networks, versus the number of nodes  $N$ . Times were measured in simulations of the same networks as those in figure 1. After first verifying that the  $\rho$  seen in simulations agrees very closely with the calculated value, we measured the mean time to fixation in those runs (out of 100) where the mutant took over. As usual the mutant fitness  $r = 2$ .

## 3. Suppression of fitness by death-first dynamics

This section builds an intuitive picture of why fitness is suppressed, in terms of an upper bound to  $\rho$ . As an aside we also give a simple explanation for why the same graph is an amplifier under the Moran process.

### 3.1. Why D-B processes suppress fitness on a star

Why are death-first processes such strong suppressors of fitness on the STAR network, and not on the fully connected one? It turns out that  $\rho$  for a D-B process is bounded above by a number proportional to  $1/N$ . The easiest way to see this is to consider the most typical events occurring under

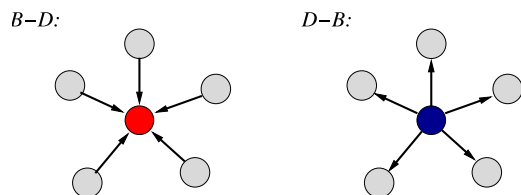


Fig. 3. Typical events on the STAR network. Under B-D dynamics the hub is 'hotter' than the spokes - it is invaded much more often. Under D-B dynamics it is the hub that does the over-writing.

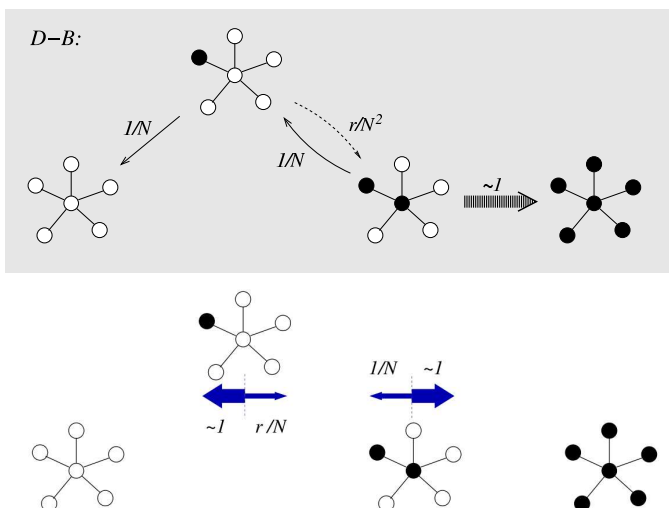


Fig. 4. *Death-birth process*. The upper figure shows approximate rates of transition away from a typical starting configuration (top-most network) in which a fitter mutant (black) occupies a spoke. Transitions that leave the state unchanged are not shown. The lower figure shows these transition rates normalised over destinations. Getting to the hub scales as only  $\sim r/N$  when compared to the probability of going extinct.

the two types of update rule, shown schematically in Figure 3.

In D-B processes the most typical event is that a spoke is chosen as the site of a death, and so most of the time the hub is the only available birth site. The hub only changes occasionally, but once a fitter mutant takes over it has a strong chance of eventual saturation. Figure 4 shows the transitions that take the system away from the most typical starting state. Because the initial site of the fitter mutant is also almost always a spoke, and spokes tend to be invaded in D-B processes, the mutant has about  $N$  times as likely to be invaded as to invade the hub itself.

For D-B updating the probability that a lone mutant at a spoke reaches the hub in any one step is  $p_{\text{hub}} = \frac{1}{N} \cdot \frac{r}{N+r-2}$  which is to be compared with the chance it goes extinct,  $p_{\text{extinct}} = \frac{1}{N}$ . Since all other transitions have no effect, and extinction is forever,

$$\rho \leq \frac{p_{\text{hub}}}{p_{\text{hub}} + p_{\text{extinct}}} = \frac{r}{N + 2(r-1)} < \frac{r}{N}$$

So  $\rho$  is now bounded *above* by  $r/N$ , whereas either in a full network or under the B-D process it is bounded *below* by  $1 - 1/r$ . This suppression of fitness is so strong as to rival the effect of having a completely uninvadable node ( $\rho \leq 1/N$ ). To put it another way, instead of the effects of fitness compounding over time and leading to a mutant with  $r = 2$  saturating about half the time, such an enhanced mutant can only expect to take over as often as two *neutral* mutants would have.

### 3.2. Why B-D processes amplify fitness on a star

A simple argument for why the Moran process amplifies fitness can be seen by constructing the equivalent of Figure 4 for B-D processes, as shown in Figure 5. In this case on a STAR the most common event is a birth at a spoke and invasion of the hub: the hub is ‘hot’ (15). This means we can think of the overall evolution of the system in terms of a slow timescale in which the number of mutant spokes changes, and an  $N$ -times faster one in which the hub flickers rapidly between being a mutant or not. Suppose that currently  $n$  out of the  $N_s$  spokes are occupied by mutants. Under B-D dynamics the hub spends a fraction  $h_r = \frac{nr}{nr + (N_s - n)}$  of the time as a mutant with fitness  $r$ , and the rest of the time it has fitness of 1. We denote the total fitness by  $F$ . The probability  $P_{\uparrow}$  that  $n$  is incremented is the chance that the hub is both occupied by a mutant ( $h_r$ ) and is chosen for birth ( $r/F$ ), times the chance that it chooses a non-mutant spoke to invade,  $(N_s - n)/N_s$ . That is,

$$P_{\uparrow} = h_r \cdot \frac{r}{F} \cdot \frac{N_s - n}{N_s}$$

The rate of decrease in  $n$  is the chance that the hub is occupied by a non-mutant ( $1 - h_r$ ) and is chosen for birth ( $1/F$ ), times the chance it chooses a mutant spoke to invade ( $n/N_s$ ), and so

$$P_{\downarrow} = (1 - h_r) \cdot \frac{1}{F} \cdot \frac{n}{N_s}$$

Comparing the two rates we see that  $P_{\uparrow} = r^2 P_{\downarrow}$ , whereas it is easily shown that for the FULL graph  $P_{\uparrow} = r P_{\downarrow}$ . Thus fitness appears to be squared in the STAR.

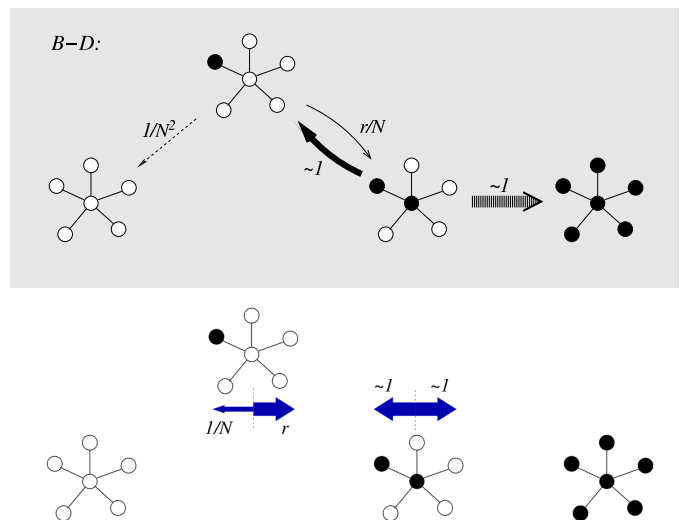


Fig. 5. *Birth-death process*, for comparison with Fig 4. The hub is very dynamic (“hot”). Although the initial state is quite likely to be returned to more than once, the birth-death process escapes it with a probability that is  $rN$  times higher than the probability of extinction.

## 4. Discussion

### 4.1. Contingency and ordering

A plausible case could be made for any of the four update dynamics discussed here in specific biological situations, and it is not obvious that any one process occupies a privileged position *a priori*. Just as different graphs may amplify or suppress the effects of fitness relative to genetic drift, so also can the different update dynamics on a given graph. It is common in biological modelling to assume that a population's size remains fairly constant, and thus that a birth (death) in some way implies a contingent death (birth).

The two types of update make different assumptions. Under B-D processes births *result in* deaths at neighbouring sites, which is uncontroversial in cases of competition for limited resources. But in D-B processes, neighbours of the death site compete for that site with a vigour that doesn't involve the number of other links they already have. Biologically this suggests scenarios such as a death freeing up resources (e.g. light for a plant) that become available for neighbours of the now-vacant site, who then compete with one another for dominance of it, with success related to their underlying fitness (12; 2).

Aside from biology, D-B or "Voter model" process are also natural models for the spread of opinions (6), language evolution (4), ecological dynamics (12), and epidemics (24). In each case individuals can be thought of as actively acquiring something from (one of) their neighbours. In such models opinion changes (for example) are in effect being instigated by the agent whose opinion is being changed: it's own previous opinion having "died", leaving a vacancy. One could have a B-D model of opinions, but that would one in which opinion changes are instigated by a source whose influence is then divided over their neighbours since they can only choose one at a time to infect. This seems less plausible in the case of opinions, but reasonable for entities that have a per-unit cost like offspring.

As an aside, note that in principle one can always turn a B-D process into an equivalent D-B process, and vice versa. For example, the probability that  $i$  invades its neighbour  $j$  under the Moran process is proportional to  $f_i/k_i$ . Instead, we could implement this by choosing a death site  $j$  first and with probability proportional to  $\sum_{l \in \{J\}} \left[ \frac{f_l}{k_l} \right]$  where  $\{J\}$  is the set of neighbours of node  $j$ . In other words a site's effective 'unfitness' is a sum over the relative fitnesses that neighbours can devote to invasions of it. Then a birth site  $i$  can be chosen with probability proportional to  $\frac{f_i}{k_i}$ . However, as this example shows, making this conversion requires that we make more complex proxies for (un)fitness that now involve the fitnesses of neighbours, whereas as a B-D process only simple local fitnesses were required. So it seems safe to separate the two families of processes in terms of the ordering ('birth-first' versus 'death-first') in practice.

### 4.2. Links as risks versus opportunities

Given the option, would an individual "want" a new link? Under B-D the answer is no, because it's just another way to be invaded, and confers no advantage in terms of being able to invade others. Under D-B the answer is yes - links mean access to new sites.

To put this more formally, we can consider a node's "nett invasion rate", which could be negative. This is its overall probability of invading a neighbour, minus its probability of being invaded itself. The incremental benefit (or otherwise) of a new link is the change to this nett rate due to the addition of a new link. As Table 1 shows, this benefit is negative for one process and positive for the other. That is, as far as the occupant of a node is concerned links are advantageous under B-D and detrimental under D-B updating. It is also interesting that the connectivity of the newly linked site is a divisor in all cases: under B-D, if you must have links, you prefer them to be to well-connected nodes, whereas under D-B you want lots of links, but would prefer them to be loners.

process	$p_{ij}$	nett invasion rate from $i$ : $p_{i*} - p_{*i}$	benefit to $i$ of link to $j$
B-D	$\frac{f_i}{k_i \bar{f}}$	$\frac{f_i}{\bar{f}} - \frac{1}{\bar{f}} \sum_{j \in \{I\}} \left[ \frac{f_j}{k_j} \right]$	$-\frac{f_j}{\bar{f}} \frac{1}{k_j}$
D-B	$\frac{f_i}{\sum_{l \in \{J\}} f_l}$	$f_i \sum_{j \in \{I\}} \left[ \sum_{l \in \{J\}} f_l \right]^{-1} - 1$	$+\frac{f_i}{\bar{f}_J} \frac{1}{k_j}$

Table 1

*Incremental benefit (or otherwise) of a new link.* The probability that the occupant of node  $i$  invades node  $j$  in any one step is  $p_{ij}$  (the  $1/N$  factor in each is omitted since it occurs everywhere).  $\bar{f}$  denotes the average fitness of the whole population,  $\{J\}$  is the set of neighbours of node  $j$ , and  $\bar{f}_J$  is the average fitness in  $\{J\}$ .  $p_{i*} = \sum_{j \in \{I\}} p_{ij}$  and is the total "export" rate from node  $i$  (its chance of invading a neighbour), whereas  $p_{*i} = \sum_{j \in \{I\}} p_{ji}$  is the corresponding rate of imports (risk of being invaded by a neighbour). The difference between these is the nett invasion rate from  $i$ . The final column is the change to the nett invasion rate that would result from a new link. (For completeness, the incremental benefits for the other two processes are  $\frac{-u_i}{\bar{u}_J} \frac{1}{k_j}$  for B-Df, and  $\frac{u_i}{\bar{u}} \frac{1}{k_j}$  for DfB).

We can use these observations to justify the use of one update rule or another in modelling invasions. If the links in a system primarily represent risks, then hubs will tend to be invaded often: a simple way to capture this tendency is therefore to model the dynamics as a Birth-Death process. In such cases fitness will play a significant role in determining evolutionary outcomes.

In other cases links may be better thought of as representing opportunities, which is another way of saying that the occupants of hubs export themselves more successfully simply by virtue of being at hubs. Death-Birth updating is one way to build in this assumption. Rather ironically,

when links are opportunities, fitnesses are much less important and evolution amounts to little more than random drift. Antal *et al.* (3) noted that a degree-heterogeneous network is an inhospitable environment under D-B dynamics. We suggest that a hub-and-spokes network (and perhaps degree-heterogeneous networks in general) *in which links are opportunities* is an inhospitable environment for evolution. On the particular network consisting of a hub and spokes, the environment is so inhospitable as to decrease the advantages of (apparent) fitness to  $1/N^{\text{th}}$  of their face value, which essentially renders the evolutionary process neutral.

It might be imagined that the question of whether deaths lead to births or vice versa is, rather like chickens and eggs, an issue of little significance. But for evolution on graphs it really does seem to matter which came first.

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