Eco-evolutionary dynamics in finite network-structured populations with migration

Abstract

A mathematical framework that describes eco-evolutionary dynamics of a network structured population with migration is developed. The effect of network structure on mutant invasion success is investigated with regards to the ecological parameter of competition and migration, where migration is conditional on group tolerance. The effect of network structure on mutant invasion with regards to these parameters is measured using the fixation probability.

Contents

1 Introduction

Mathematical models are being developed to unravel the world around us, for example, characterising evolution of important biological processes. The amount of available information and the set of assumptions that modellers make give rise to variety of models. These models are then used to draw conclusions. The question that whether these conclusion are correct and useful depend on two questions: what we want from the model and what are the assumptions on which we have build the model? Traditionally models of evolutionary dynamics have been build by assuming homogeneous population with some exceptions of spatially distributed population. However, Lieberman et al. (2005) introduced evolutionary graph theory (EGT) to see how the structure in the population affects the evolutionary dynamics. In fact, the structure in the population has a key role as not all individuals are connected with each other also the rate of state transitions are not the same for all individuals. Constructing models over a network cover these two deficiencies in the classical models.

Typically, in evolutionary graph theory, each vertex represents an individual and the weight of the edge gives the rate at which individual place its offspring into adjacent vertices. However, we can think of it as the graph or network in which a node/edge is represented by an individual or state of an individual and the link or edge between two nodes describe the interaction between individuals or transition from one state to another. In a fixed population structure the network is assumed fixed and every individual can occupy exactly one node. However, in order to represent meta population, in which individuals are distributed in distinct but connected sites, we can think of a network such that a single node can be occupied by more than one individuals. Recently, some interesting models were developed for the eco-evolutionary dynamics of such population. Specifically, Pattni et al. (2021) constructed a birth-death model for such a population. They attempt to uncover the underlying ecological and evolutionary dynamics. They also identify some conditions under which evolutionary graph theory can be achieved. This framework, otherwise quite general, has some limitations. For example, they consider coupled birth and movement events which means that new born individuals immediately move to a neighbouring place. Another explanation to this coupled birth and movement assumption could be that individual place their offspring in the neighbouring sites.

We aim to consider a more realistic ecological scenario in which these both birth and death dynamics are decoupled. In such a scenario offspring will be placed in the same site as their parent and any individual will be able to move anytime. The movement between sites can be motivated by several factors such as environmental conditions and to avoid competition for

food, finding mate or better place for breeding. Some attempts have been made to model such ecological dynamics but there are always some very strict assumptions on how the individuals will between the sites. For examples, some author have considered striations in which individual can move to the common territory or only immediate neighboring sites. In some models, movements are restricted by home range. However, its more realistic can move to any connected site and need not to return to home site. We consider density-dependent movement, where two special cases are considered, low tolerance to group members and high tolerance to group members. For low group tolerance, individuals are highly sensitive to their group members and would choose to move away if unfavourable. Where as with high group tolerance, individuals move independently of their current group as they are insensitive to them.

2 Modelling Framework

We assume that the individuals in the population are spread in distinct but connected sites of a fixed network. The sites of the network can have no, one or many individuals at a given time. The population size and composition keep changing due to births, deaths and movements between the sites. The composition of the population changes either due to variations in rates for different types of individuals or the possibility of new mutant appearance.

To mathematically describe such populations, we use the Champagnat et al. (2006) model with network structure as described in Pattni et al. (2021). Individuals can have l real-valued traits contained within the set $\mathcal{U} \subset \mathbb{R}^l$. The sites that individuals can occupy is given by set $\mathcal{X} = \{1, \ldots, N\}$. The characteristics of an individual are given by $i = (U_i, X_i)$ where $U_i \in \mathcal{U}$ and $X_i \in \mathcal{X}$. An individual with characteristics i is denoted I_i. The state of the population is given by a multi-set $\mathcal{S}$, which means that for each individual with characteristics i there is a copy of i in $\mathcal{S}$. Formally, we would write this as $\{i^{m(i)} : i \in \mathcal{I}, \mathcal{I} \subseteq \mathcal{U} \times \mathcal{X}\}$ where $m : \mathcal{I} \to \mathbb{Z}^+$ is the multiplicity (number of occurrences) of i. Individuals in the same site are given by set $\mathcal{S}_n = \{i \in \mathcal{S} : X_i = n\}$.

The connections between sites are given by a directed and weighted network represented by a matrix W with entries $W_{m,n} \geq 0$. An individual can move from site m to n if site m is connected to site n, that is, $W_{m,n} > 0$. In Pattni et al. (2021), birth and movement were coupled such that an offspring can be placed onto a connected site. Here, we consider uncoupled birth and movement. Individuals are assumed to reproduce asexually such that they place their offspring on the same site. The rate at which individual I_i gives birth is given by $b(i, \mathcal{S}, W)$. If there is no mutation, the offspring of individual I_i has characteristics $i = (U_i, X_i)$. With probability $\mu(i)$, individual I_i gives birth to an offspring with mutation. In this case, the probability that the I_i gives birth to an offspring with trait u is $M(U_i, u)$ such that $M(U_i, u) = 0$ if $u \notin \mathcal{U}$. The

Table 1: Summary: Notations for framework, and their definitions and descriptions.

Notation	Definition	Description
N	$N \geq 1$	Number of distinct sites
W	$W_{m,n} \geq 0$	Matrix represent network of N distinct sites
$\mathcal{U}$	$\mathcal{U} \subset \mathbb{R}^l$	l real-valued phenotypic traits of an individual
$\mathcal{X}$	$\mathcal{X} = \{1, \ldots, N\}$	Set of positions an individuals can occupy
$i = (U_i, X_i)$	$U_i \in \mathcal{U}$, $X_i \in \mathcal{X}$	The trait i of the individual I
I_i	$i \in \mathcal{U} \times \mathcal{X}$	An individual I with traits i
$\mathcal{S}$	Multiset	State of the population that containing traits of each individual
$\mathcal{S}_n$	$\mathcal{S}_n = \{i \in \mathcal{S} : X_i = n\}$	Represent the individual in site n, therefore, $\mathcal{S}_n \subseteq \mathcal{S}$.
$d(i, \mathcal{S})$	$d \geq 0$	Death rate of I_i
$b(i, \mathcal{S})$	$b \geq 0$	Birth rate of I_i
$\mu(i)$	$\mu \geq 0$	Probability that an offspring I_i carries a mutation
$M(U_i, u)$	$M \geq 0$ and $i, U_i \in \mathcal{U}$	Probability that I_i gives birth to an offspring with trait $u \notin \mathcal{U}$
$m(i, x, \mathcal{S})$	$m \geq 0$	Net movement rate to site x
ϕ	$\phi : \{\mathcal{S}_\lambda\} \longrightarrow \mathbb{R}$	Real-valued bounded function that act on the states of the system
$\mathcal{L}$	Generator	Describes how the expected values of functions ϕ of a Markov process change in infinitesimal time intervals

rate at which individual I_i dies is given by $d(i, \mathcal{S}, W)$. The rate at which individual I_i moves to site x is given by $m(i, x, \mathcal{S}, W)$. Since W is constant, we respectively use $b(i, \mathcal{S})$, $d(i, \mathcal{S})$ and $m(i, x, \mathcal{S})$ for the birth, death and movement rate for brevity.

The evolution of the population is described by a continuous time Markov process. The generator $\mathcal{L}$ that acts on real bounded functions $\phi(\mathcal{S})$ that describes the infinitesimal dynamics of the state of the population at time t is given by

$$\begin{aligned}\mathcal{L}\phi(\mathcal{S}) = &\sum_{i\in\mathcal{S}}[1-\mu(i)]b(i,\mathcal{S})[\phi(\mathcal{S}\cup\{i\})-\phi(\mathcal{S})]\\ &+\sum_{i\in\mathcal{S}}\mu(i)b(i,\mathcal{S})\int_{\mathbb{R}^l}[\phi(\mathcal{S}\cup\{(u,X_i)\})-\phi(\mathcal{S})]M(U_i,u)du\\ &+\sum_{i\in\mathcal{S}}d(i,\mathcal{S})[\phi(\mathcal{S}\backslash\{i\})-\phi(\mathcal{S})]\\ &+\sum_{i\in\mathcal{S}}\sum_{x\in\mathcal{X}}m(i,x,\mathcal{S})[\phi(\mathcal{S}\cup\{(U_i,x)\}\backslash\{i\}-\phi(\mathcal{S})].\end{aligned} \tag{1}$$

In the equation above, the first line describes birth without mutation, the second line describes birth with mutation, the third line describes death and the fourth line describes movement.

For the Markov process described by the infinitesimal dynamics in equation (1), the key quantity we are interested in is the hitting probability. The probability of $h_{\mathcal{A}}(\mathcal{S})$ of starting in state $\mathcal{S}$ and hitting a state in set $\mathcal{A}$ is calculated as follows

$$\begin{cases}\mathcal{L}h_{\mathcal{A}}(\mathcal{S})=0 & \mathcal{S}\notin\mathcal{A}\\ h_{\mathcal{A}}(\mathcal{S})=1 & \mathcal{S}\in\mathcal{A}.\end{cases} \tag{2}$$

Derivation of this is given in the appendix.

2.1 Evolutionary Scenario Considered

The evolutionary scenario considered is one where a population of residents is invaded by a mutant. In particular, we consider the case where the $\mu \to 0$ so that the population evolves through adaptive sweeps. This means that once a mutant arises in a resident population, either all residents or all mutants completely die out before another mutant arises in the population. The type that remains is said to have fixated in the population. Formally, we consider two types of individuals in the population, the residents (type R) and mutants (type M), that is, $\mathcal{U} = \{R, M\}$. The set of states where all individuals are residents is given by $\mathcal{R} = \{\mathcal{S} : U_i = R,\ \forall i \in \mathcal{S}\}$, similarly the set of all states with mutants is given by $\mathcal{M} = \{\mathcal{S} : U_i = M,\ \forall i \in \mathcal{S}\}$. We are interested in calculating the probability a resident population is replaced by the mutant

type. The probability of mutants fixating is obtained by solving for the hitting probability as follows,

$$\begin{cases} \mathcal{L}h_{\mathcal{M}}(\mathcal{S}) = 0 & \mathcal{S} \notin \mathcal{M} \cup \mathcal{R} \\ h_{\mathcal{M}}(\mathcal{S}) = 1 & \mathcal{S} \in \mathcal{M} \\ h_{\mathcal{M}}(\mathcal{S}) = 0 & \mathcal{S} \in \mathcal{R} \end{cases} \tag{3}$$

When mutants fixate from an initial state with one mutant, it is called the fixation probability. Since there are multiple states with one mutant, we calculate the average fixation probability as follows

$$\rho = \sum_{\mathcal{S} \in \mathcal{R}} \sum_{x \in \mathcal{X}} p_{x,\mathcal{S}} h_{\mathcal{M}}(\mathcal{S} \cup \{(M, x)\}) \tag{4}$$

where $p_{x,\mathcal{S}}$ is the mutant appearance distribution (MAD), i.e. the probability that a mutant appears in site x when the population is in state $\mathcal{S}$.

3 Birth-Death-Migration Model

To apply the modelling framework, we consider a birth-death-migration model that we can use to calculate the fixation probability. The birth rate is considered to be fixed and depends only on the type of individual, that is,

$$b(i, \mathcal{S}) = \beta_{U_i}. \tag{5}$$

The death rate is given by

$$d(i, \mathcal{S}) = \delta_i + \sum_{j \in \mathcal{S}_{X_i} \setminus \{i\}} \gamma_{U_i, U_j} \tag{6}$$

where δ_u is the natural death rate of a type u individual and $\gamma_{u,v}$ is the death rate of a type u individual when competing with a type v individual.

We assume that individuals move with migration rate $\lambda > 0$. Where they move to will depend upon the structure of the network given by W. For the networks considered, we assume that $W_{x,x} = 0$ and $\sum_{y \in \mathcal{X}} W_{x,y} = 1 \ \forall x \in \mathcal{X}$, that is, all diagonal element of W are zero and W is right-stochastic. This means that $W_{x,y}$ is the probability of migrating from site x to y. We will consider density-dependent movement given by the following sigmoid function adapted from Pattni et al. (2018),

$$m(i, x, \mathcal{S}) = \left(1 - \frac{\alpha}{\alpha + (1 - \alpha)\tau^{g(i, \mathcal{S}_{X_i})}}\right) \lambda W_{X_i, x}. \tag{7}$$

Here, α is the probability that the focal individual i stays in its current site, τ is the tolerance to other members in the same site and $g(i, \mathcal{S}_{X_i})$ is the benefit of individual i being in group $\mathcal{S}_{X_i}$. For this density-dependent movement function, the following two limiting cases are of note.

1. **High tolerance to group members ($\tau \to 1$):** In this case individuals move independently of one another as the benefit of being in a group has virtually no impact. The movement rate is given by

$$m(i, x, \mathcal{S}) = (1 - \alpha)\lambda W_{X_i,x}. \tag{8}$$

2. **Low tolerance to group members ($\tau \to 0$):** In this case the focal individual will stay if its current group is beneficial, i.e. if $g(i, \mathcal{S}_{X_i}) > 0$, but can move otherwise. The movement rate is given by

$$m(i, x, \mathcal{S}) = \begin{cases} \lambda W_{X_i,x} & g(i, \mathcal{S}_{X_i}) < 0, \\ (1 - \alpha)\lambda W_{X_i,x} & g(i, \mathcal{S}_{X_i}) = 0, \\ 0 & g(i, \mathcal{S}_{X_i}) > 0. \end{cases} \tag{9}$$

3.1 Example of birth-death-migration model

We consider the following parameters as an example of the birth-death-migration model. The birth rate of a resident is $\beta_R = 1$ and mutant is $\beta_M = 2$, unless specified otherwise. It is assumed that individual cannot die naturally, i.e. $\delta_u = 0$ for $u = M, R$. This is to prevent the population going extinct. Alternatively, we can assume that the population is reseeded when there is an extinction event. However, we want to avoid this technicality for now. Death due to competition is assumed to be identical for all paired types, i.e. $\gamma_{u,v} = \gamma,\ \forall u, v$. This means that the residents and mutants differ with respect to their birth rate only.

For density-dependent movement, we will consider the following group benefit function

$$g(i, \mathcal{S}_{X_i}) = \begin{cases} 1 & |\mathcal{S}_{X_i}| = 1, \\ -1 & |\mathcal{S}_{X_i}| > 1. \end{cases} \tag{10}$$

In this case the focal individual benefits when they are alone. We only consider the limiting cases highlighted above and, for simplicity, we assume that probability of staying is small ($\alpha \ll 1$), which means it has negligible impact. The movement rate for high group tolerance is given by

$$m(i, x, \mathcal{S}) = \lambda W_{X_i,x}, \tag{11}$$

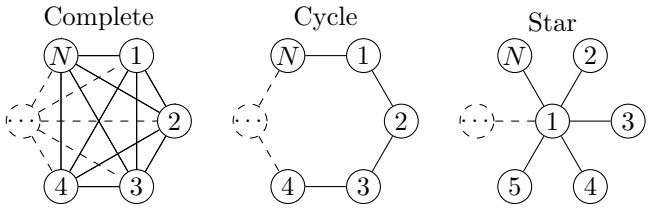

Figure 1: Networks considered in this paper. Each node represents a site. N is the total number of sites. Each edge represents an incoming and outgoing weighted edges whose weights are given by W. Edges represent the migration of individuals. In the star network site 1 is called the centre and sites 2 to N are called leaf sites.

and for low group tolerance by

$$m(i,x,\mathcal{S}) = \begin{cases} \lambda W_{X_i,x} & |\mathcal{S}_{X_i}| > 1, \\ 0 & |\mathcal{S}_{X_i}| = 1. \end{cases} \tag{12}$$

The complete, cycle and star networks will be considered, they are illustrated in figure 1. For each network W the non-zero weights are follows

$$\left.\begin{array}{l} \text{Complete: } W_{ij} = 1/(N-1),\ i \neq j \text{ and } i,j \in \mathcal{X}, \\ \text{Cycle: } W_{i,i+1} = W_{j,j-1} = W_{1,N} = W_{N,1} = \frac{1}{2},\ i = 1,\ldots,N-1 \text{ and } j = 2,\ldots,N, \\ \text{Star: } W_{1,i} = \frac{1}{N-1},\ W_{i,1} = 1,\ i = 2,\ldots,N-1. \end{array}\right\} \tag{13}$$

Note that for all networks $W_{ii} = 0$ for $i \in \mathcal{X}$, this is because individuals are born on the same site as their parent and will remain there until they die or migrate. The complete and cycle networks are circulations Lieberman et al. (2005), which means that the sum of the incoming and outgoing weights for each site are the same, i.e. $\sum_i W_{i,j} = \sum_j W_{j,i} \quad \forall i,j \in \mathcal{X}$.

3.2 Simulating birth-death-migration model

To simulate the fixation probability in the birth-death-migration model we need to determine the initial states of the population. In cases where the population size is fixed, such as in evolutionary graph theory (Lieberman et al. 2005) and its various extensions (Pattni et al. 2017, Yagoobi & Traulsen 2021), a mutant is introduced into the population by randomly replacing a resident individual as it keeps the model intact. One way to implement this scheme here would be to assume that the population starts in a given resident state and we then replace one resident with a mutant. This approach was used in Pattni et al. (2021) where the initial state consisted of one resident occupying each site. This approach is simplistic and sufficed for the purpose of understanding how evolutionary graph theory dynamics can be derived from a

model with eco-evolutionary dynamics. A more realistic approach is to initialise the population in a state that is representative of the low mutation limit ($\mu \to 0$). We pursue this option here.

The brute force option to initialise a population in the low mutation limit is to run a simulation with a low mutation rate that is representative of the low mutation limit. This carries an additional computation cost that is preferably avoided. We therefore start with a resident population given by column vector $\mathbf{x}$ where x_n is the number of residents in site n. To choose $\mathbf{x}$ close to the equilibrium state of residents in the low mutation limit we solve,

$$0 = \beta_R \mathbf{x} - \gamma \mathbf{x} \circ (\mathbf{x} - 1) + W^\intercal(\mathbf{x} \circ m(\mathbf{x})) - (W\mathbf{1}) \circ (\mathbf{x} \circ m(\mathbf{x})), \tag{14}$$

where $\mathbf{1}$ is the column vector of 1s, $\circ$ is Hadamard multiplication and $m(\mathbf{x})$ gives a column vector with the movement rates. We then set the mutation rate to $\mu = 0.01$ and run the simulation until a mutant appears. Once a mutant appears, we set $\mu = 0$ and continue the simulation till fixation. This is one run of the simulation which we repeat for the number of simulations required.

Initialising the population in this way ensures that a mutant appears in site x in state $\mathcal{S} \in \mathcal{R}$ proportional to $|\mathcal{S}_x| p_{\mathcal{S}}$, i.e. the probability of being in state $\mathcal{S}$ ($p_{\mathcal{S}}$) weighted by the number of resident individuals in site x in that state ($|\mathcal{S}|_x$). Note that a resident individual is likely to appear in a site with a higher expected number of individuals.

4 The Low Migration Limit ($\lambda \to 0$)

We first consider the case with low migration rate, $\lambda \to 0$. In this case a site will reach fixation before a migration event happens and therefore each site can be viewed as either a resident or mutant site. The probability that a mutant fixates is then a two step process. First, an initial mutant appears on a site and fixates there. Second, mutants then spread until they fixate in the population. This approach has been used in the case of fixed population size within patches (Pattni et al. 2017, Yagoobi & Traulsen 2021).

For the birth-death-migration model we consider, each site can be treated independently such that the state of each site is given by the number of mutants or residents on that site. The probability that a mutant initially appears in site x and fixates there is given by

$$\rho_{M,x}^{\text{Init}} = \frac{\sum_{n=1}^{\infty} n \pi_{n,x}^R h_{\mathcal{M}}(\{(0,x)^n, (1,x)\})}{\sum_{n=1}^{\infty} n \pi_{n,x}^R}, \tag{15}$$

where $\pi^R_{n,x}$ is the probability that there are n residents in site x. Let $J^u_{x,y}$ be the rate at which a type u individuals migrates from site x to y. For high group tolerance, this is given by

$$J^u_{x,y} = \lambda W_{x,y} \sum_{n=1}^{\infty} n\pi^u_{n,x} = \lambda W_{x,y} \mathbb{E}(\text{Groups of size 1 or more in site } x), \tag{16}$$

and low group tolerance we have

$$J^u_{x,y} = \lambda W_{x,y} \sum_{n=2}^{\infty} n\pi^u_{n,x} = \lambda W_{x,y} \mathbb{E}(\text{Groups of size 2 or more in site } x). \tag{17}$$

Note the difference, for low group tolerance there should be at least two individuals on a site for a migration event to take place. The probability with which a type u immigrant fixates is given by

$$\rho^{\text{Mig}}_{u,x} = \sum_{n=0}^{\infty} \pi^v_{n,x} h_{\mathcal{F}(u)}(\{(v,x)^n, (u,x)\}) \tag{18}$$

where $v \in \{M, R\} \setminus \{u\}$, $\mathcal{F}(M) = \mathcal{M}$, and $\mathcal{F}(R) = \mathcal{R}$. Let $s \subset \mathcal{X}$ represent the state where all $x \in s$ represent mutant sites. The fixation probability of a mutant is then given by solving the following recursive equation

$$\rho^{\text{Low Mig}}_s = \sum_{s' \subset \mathcal{X}} P_{ss'} \rho^{\text{Low Mig}}_{s'}$$

with boundary conditions $\rho_\emptyset = 0$ and $\rho_{\mathcal{X}} = 1$, and

$$P_{ss'} = \begin{cases} \sum_{x \notin s} J^R_{x,y} \rho^{\text{Mig}}_{R,y} & \text{if } s' = s \setminus \{y\} \text{ for } y \in s, \\ \sum_{x \in s} J^M_{x,y} \rho^{\text{Mig}}_{M,y} & \text{if } s' = s \cup \{y\} \text{ for } y \notin s, \\ 0 & \text{otherwise.} \end{cases}$$

The average fixation probability of a mutant is then given by

$$\rho = \sum_{x \in \mathcal{X}} \rho^{\text{Init}}_{M,x} \rho^{\text{Low Mig}}_{\{x\}}.$$

We can solve for h in ρ^{Mig} and ρ^{Init} using equation (3) provided we assume that there is an upper limit K for the carrying capacity of a site. In particular, the upper limit is chosen so that the probability of reaching this limit is essentially 0. We therefore only have to consider those population states $\mathcal{S}$ such that $|\mathcal{S}| \leq K$. An analytical expression for π can be obtained

for low tolerance to group members as there is always at least one individual on a site. It is given by,

$$\pi^u_{n,x} = \frac{(\beta_u/\gamma)^n}{n!}\frac{1}{\exp(\beta_u/\gamma)-1} \tag{19}$$

as shown in PAPER ON SINGLE SITE. This gives

$$\begin{aligned}
&\sum_{n=1}^{\infty} n\pi^u_{n,x} = \frac{\beta_u/\gamma}{1-\exp(-\beta_u/\gamma)},\\
&\rho^{\text{Init}}_{M,x} = \sum_{n=1}^{\infty}\frac{(\beta_R/\gamma)^{n-1}}{n!\exp(\beta_R/\gamma)} h_{\mathcal{M}}(\{(0,x)^n,(1,x)\}),\\
&J^u_{x,y} = \lambda W_{x,y}\beta_u/\gamma.
\end{aligned}$$

Using these equations we can analytically solve for the fixation probability for low group tolerance. For high group tolerance, obtaining an analytical expression is difficult as there can be empty sites. We therefore simulate the fixation probability for high group tolerance.

For circulation networks, the fixation probability is given by

$$\rho^{\text{Init}}_M \rho^{\text{Moran}}(N,r), \tag{20}$$

where N is the number of sites, $\rho^{\text{Moran}}(N,r)$ is the Moran probability, which is given by

$$\rho^{\text{Moran}}(n,r) = \frac{1-\frac{1}{r}}{1-\frac{1}{r^N}}, \tag{21}$$

and r is the advantage of mutants relative to residents, which is given by

$$r = \frac{\mathbb{E}(\text{Mutants in a site that can migrate})\rho^{\text{Mig}}_M}{\mathbb{E}(\text{Residents in a site that can migrate})\rho^{\text{Mig}}_R}. \tag{22}$$

Note that the index for site is dropped because in circulations each mutant or resident site is identical to one another.

For low group tolerance, figure 2 (a) shows that an increasing competition rate decreases the fixation probability for a low movement rate for all networks. To understand why this is the case, we first look at the fixation probability in circulation networks (complete and cycle) where the analytical calculation, which we see is in agreement with the simulations, can be used to explain this. In the analytical calculation given by equation (20) there are two components. The first component, ρ^{Init}_M, describes the intra-site dynamics, that is, how a mutant fixates in a single site. The intra-site dynamics resemble dB EGT dynamics as shown in figure 2 (c). The formula for dB EGT dynamics, is given by (Kaveh et al. 2015, Hindersin & Traulsen 2015)

$$\rho^{\text{dB}} = \frac{N-1}{N}\frac{1-\frac{1}{r}}{1-\frac{1}{r^{N-1}}} \tag{23}$$

where N is the number of individuals/sites and r is the relative fitness of an individual. The intra-site dynamics are approximated using dB evolutionary dynamics by setting $r = \frac{\beta_M}{\beta_R} = 2$ and $N = E_R + 1$ since E_R is approximately the number of residents that would be present on a site when a mutant arises. The second component, ρ^{Moran}, describes the inter-site dynamics, or how mutants spread once they have fixated on a single site. The inter-site dynamics are shown in figure 2 (d), where we see that the fixation probability is a sigmoid shape curve that converges to 1 as the competition rate decreases and converges to 0.5 as the competition rate decreases. This implies that for a low competition rate a mutant fixating on one site is sufficient to guarantee that it goes on to fixate in the entire population. This is explained by the forward bias (r), given by equation (22), which is the rate at which a mutant site increases by 1 divided by the rate at which a resident site increases by 1. Figure 2 (e) shows that the forward bias exponentially increases as the competition rate decreases. In the cases where the competition rate decreases, we have that

$$\lim_{\gamma\to\infty} r = \lim_{\gamma\to\infty} \frac{\pi_2^M \rho_M^{\text{Mig}}}{\pi_2^R \rho_R^{\text{Mig}}} = \lim_{\gamma\to\infty} \frac{\frac{(\beta_M/\gamma)^2}{2!}\frac{1}{\exp(\beta_M/\gamma)-1}\frac{(\beta_R/\gamma)^1}{1!}\frac{1}{\exp(\beta_R/\gamma)-1}\frac{1}{2}}{\frac{(\beta_R/\gamma)^2}{2!}\frac{1}{\exp(\beta_R/\gamma)-1}\frac{(\beta_M/\gamma)^1}{1!}\frac{1}{\exp(\beta_M/\gamma)-1}\frac{1}{2}} = \frac{\beta_M}{\beta_R},$$

this is obtained by assuming that there are two individuals when a migration event happens and that an immigrant arrives to a site with one individual only. Putting the two components together gives the following properties for circulation networks,

$$\lim_{\gamma\to\infty} \rho_M^{\text{Init}} \rho^{\text{Moran}}(N, r) = \frac{1}{2}\rho^{\text{Moran}}\left(N, \frac{\beta_M}{\beta_R}\right), \tag{24}$$

$$\lim_{\gamma\to 0} \rho_M^{\text{Init}} \rho^{\text{Moran}}(N, r) = 1 - \frac{\beta_R}{\beta_M} \tag{25}$$

where N is the number of sites and r is given by equation (22).

In the star network for low group tolerance figure 2 (a) shows that it follows a similar pattern to the complete and cycle networks. However, the fixation probability in the star network is higher for high competition rates but converges as the competition rate decreases. Since $\lambda \to 0$, mutants are likely to appear on leaf sites in a star network as the combined number of individuals on leaf sites is higher than the centre site. Appearing on leaf sites is beneficial because the way in which W is defined for the star network (equation (13)) allows leaf sites to act as source sites, i.e. are net exporters of individuals, (Pattni et al. 2021). For low competition rate convergence occurs since the intra-site dynamics are identical for all networks and, as explained earlier, if a mutant fixates on one site, it is essentially guaranteed to fixate in the entire population. On the other hand, as the competition rate increases, which gives residents a better chance to prevent invasion, the divergence in the fixation probability between the star and circulation networks becomes more apparent.

For high group tolerance, figures 2 (b) shows a similar pattern to low group tolerance where fixation probability decreases as the competition rate increases. High group tolerance allows empty sites, however, when competition rate is low, the likelihood of empty sites deceases and the intra-site dynamics would be similar to that of low group tolerance. The fixation probabilities are therefore identical to the low group tolerance case for low competition rate. As the competition rate increases, the chance of having empty sites increases, changing the behaviour observed. In particular, the population starts converging to a population size of 1 as individuals start dying off when they meet. This means that as the competition rate increases the fixation probability starts converging to a $\frac{1}{2}$ as the likelihood that a mutant appears in a population with one resident increases. Overall, the fixation probability start decreasing then increasing again as the competition rate increases.

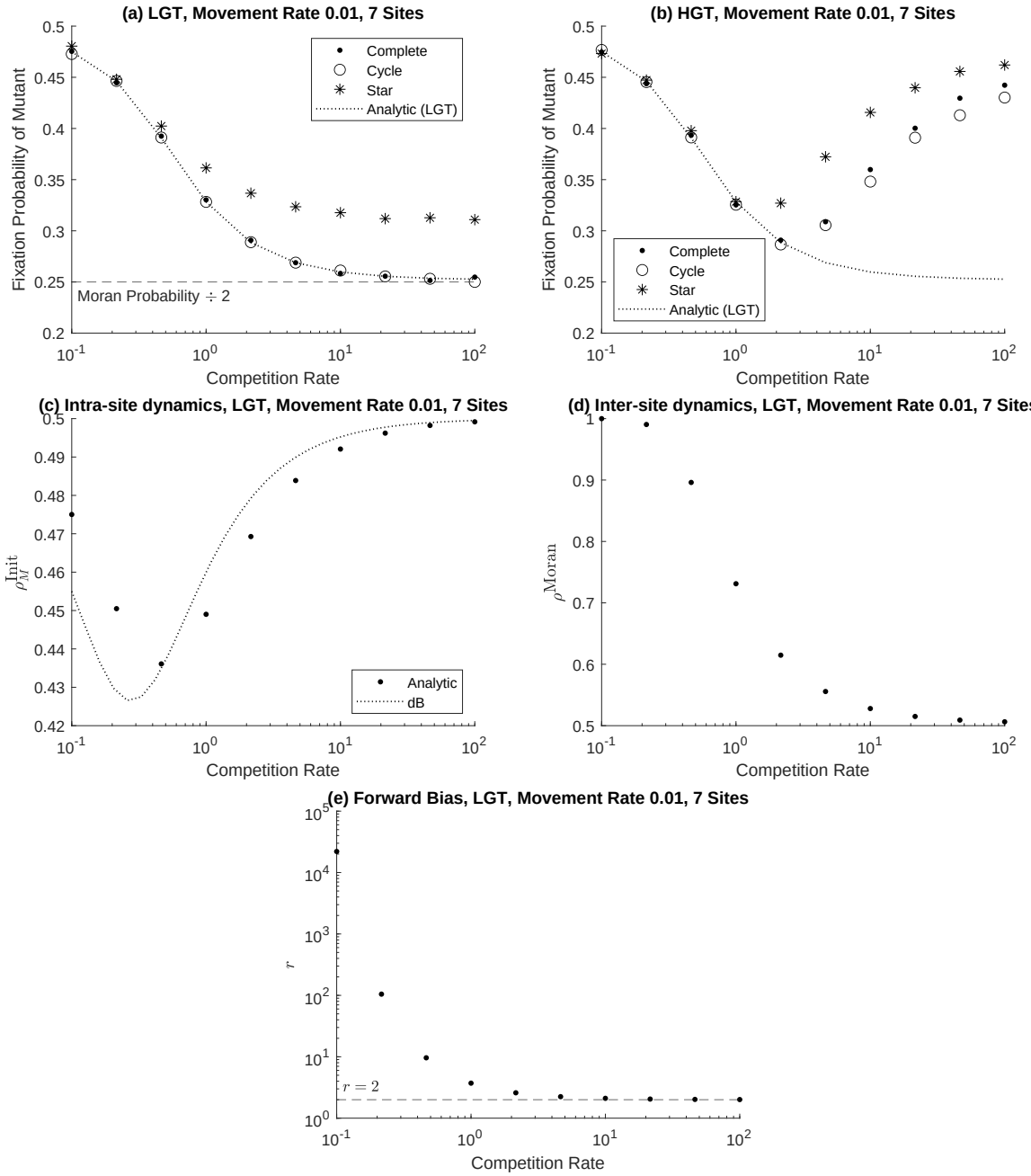

Figure 2: Fixation probability of a mutant plotted against competition rate for low movement. Calculation of analytic plot is given by equation (20). LGT: low group tolerance. HGT: high group tolerance.

5 General Migration Rate

In this section we consider the case for a general migration rate ($\lambda > 0$). The fixation probability in this case is calculated via simulation.

5.1 Effect of increasing migration rate

Figure 3 shows that the fixation probability increases with the migration rate. Migration allows individuals to escape competition and this effect depends upon the competition rate, network structure and group tolerance.

For low group tolerance, figure 3 (a–d) shows that as the migration rate increases the fixation probability starts increasing and plateaus earlier for low competition than high competition. However, as $\lambda \to \infty$ there would be a larger overall increase in the fixation probability for high competition. In the initial growth and plateau phases of the fixation probability, the complete and cycle networks follow each other closely and are indistinguishable. As the growth in the fixation probability accelerates, there is higher acceleration in the complete network than the cycle network. The key factor here is local correlation between groups on neighbouring sites on the cycle. For low migration rates fixation probabilities are low and similar for both cycle and complete networks. New individuals are likely to be born into bigger groups, as there are more potential parents, but cannot move on, so face increased competition. As they hardly move, network does not matter. For intermediate movement rates fixation probabilities are intermediate, but differ for the two types. New individuals are born to bigger groups, but there is some dispersal so they face an intermediate level of competition. Here dispersal happens to some extent, and so the network does matter. For high movement rates fixation probabilities are high and similar for the two types. New individuals are born in bigger groups but then there is rapid dispersal so they live in 'average' groups. As movement is so far they mix well, so network does not matter. To illustrate this point further, figure 4 shows the fixation probability in the case of a neutral mutant, i.e. $\beta_R = \beta_M = 1$. If there was no correlation between the sites, the fixation probability would be identical for the complete and cycle networks. There is correlation as we see a difference in the fixation probabilities, which happens for intermediate movement rates. For the star network, as λ increases we see that there is an initial dip in the fixation probability before it starts increasing. This is because increasing the movement rate results in the number of individuals in the centre site becoming larger than all the leaf sites combined. A mutant is therefore likely to appear in the centre site which is a sink, i.e. a net importer of individuals, which adversely affects the fixation probability Pattni et al. (2021). This dip happens earlier for a lower competition rate and, after this dip, the fixation probability remains below that of the complete and cycle networks.

For high group tolerance figure 3 (e–h) shows that the behaviour observed is similar to to low group tolerance when competition rate is low but vastly different for a higher competition rate. For low competition rate, the intra-site dynamics are similar in high and low group tolerance. In particular, for a low competition rate the likelihood of there being empty sites is low even as the migration rate increases. On the other hand, for a high competition rate the likelihood of empty sites increases. This means that a mutant is arises in a population with fewer individuals that in the low group tolerance case. This is observed in figure 3 (g) and (h). In (g), the star network has a higher fixation probability for all migration rates than the complete and cycle networks. This is because individuals are more likely to meet in the centre site resulting in death due to competition, which drives the population size down. This effect is substantial for a high competition rate as seen in (h). As the movement rate increases, the fixation probability in all networks swiftly converges to $\frac{1}{2}$ since the population size is converging to 1.

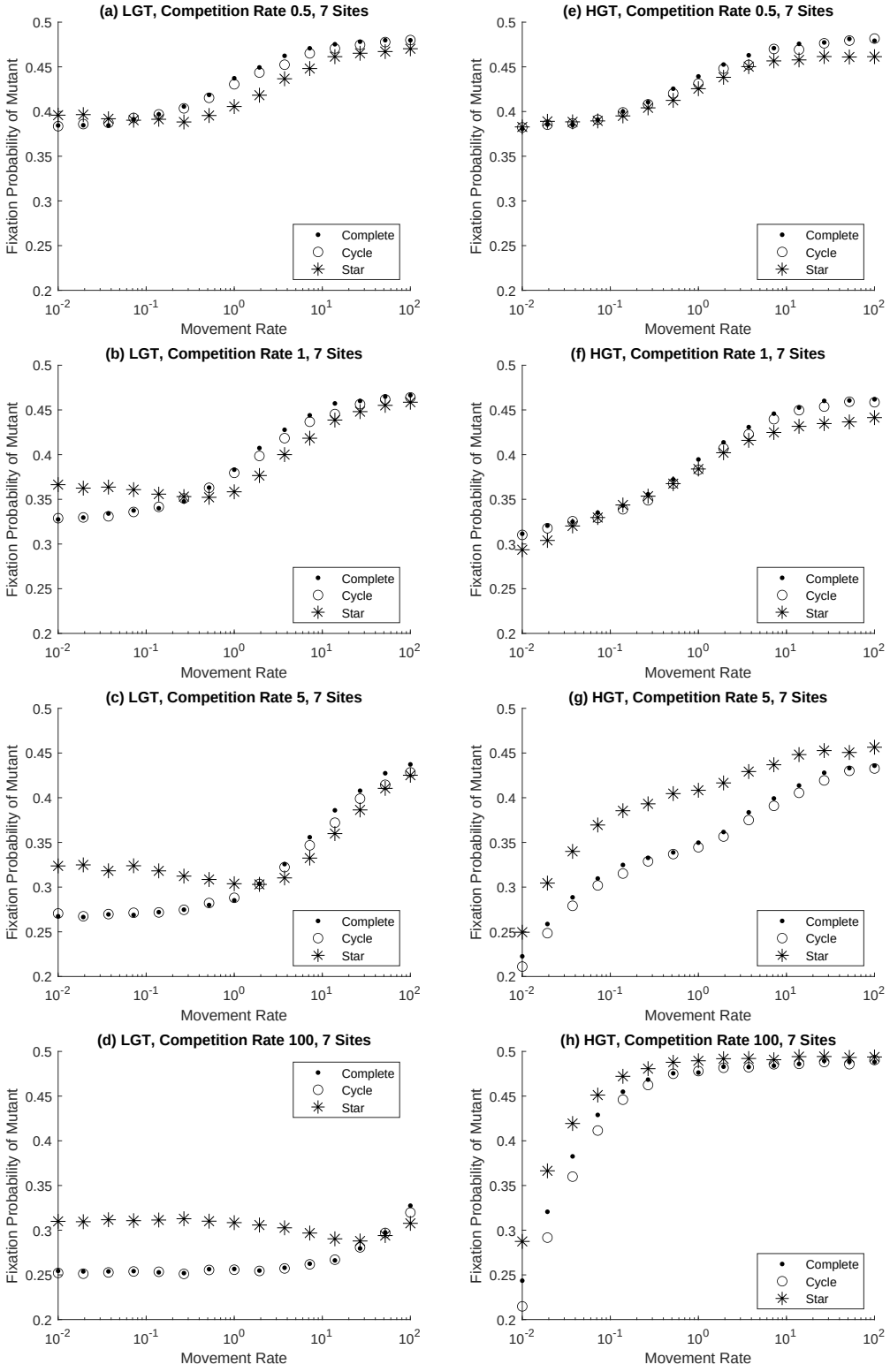

Figure 3: Fixation probability of a mutant plotted against the movement rate of individuals for different competition rates. Each network has 7 sites and birth rate of mutants is 2. Figures (a–d) there is low group tolerance. Figures (e–g) there is high group tolerance.

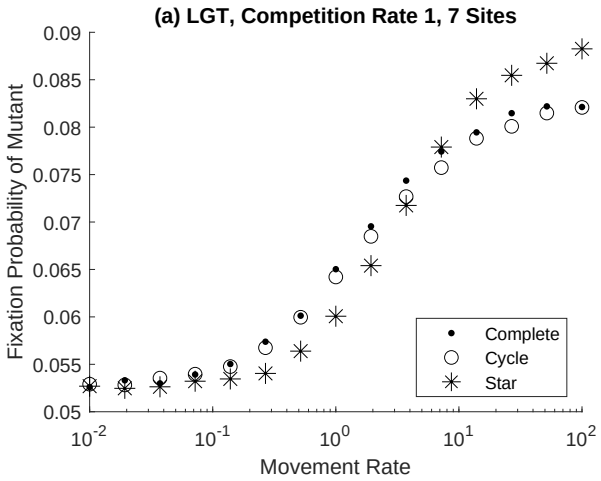

Figure 4: Fixation probability in the neutral case. This plot was generated using 10^6 simulations.

5.2 Comparison to Low Migration Limit ($\lambda \to 0$)

For low group tolerance Figure 5 (a–c) shows that there is initially similar behaviour to the low migration limit, but gradually breaks down as the movement rate keeps increasing. The fixation probability in the complete and cycle networks are higher than in the low migration limit as migration enables escaping competition. This difference is less apparent for high competition as it requires a much larger movement rate to make a significant difference. In the low migration limit, the star network has a higher fixation probability than the complete and cycle networks, and converges as the competition rate decreases. Here, the star network initially has a lower fixation probability for a low competition rate. As the competition rate increases this difference gradually diminishes and eventually the fixation probability surpasses that of the complete and cycle networks. This behaviour is explained by where the initial mutant appears in the star network. When the competition rate is low, there are more individuals in the centre site than there are on leaf sites, thereby increasing the likelihood of a mutant appearing on the centre site. The centre site acts as a sink, i.e. it is a net importer of individuals (Broom & Rychtář 2008, Pattni et al. 2021), which is less beneficial for a mutant that is trying to spread. As the competition rate increases, the number of individuals in the centre site decreases and the number of individuals in the leaf sites increases. A mutant is therefore more likely to appear on a leaf site, which acts as a source site, i.e. a net exporter of individuals, which helps the spread of mutants.

For high group tolerance figure 5 (d–f) shows that the fixation probability decreases then increases as the competition rate increases. This behaviour is significantly different to that

observed in the low migration limit. For low competition rate ($\gamma \leq 1$) the behaviour is similar to that of low group tolerance (figure 5 (a–c)), this means that the intra-site dynamics are similar for both cases. That is, even though high group tolerance allows for empty sites in their intra-site dynamics, this is unlikely when the competition rate is lower. As the competition increases ($\gamma > 1$), empty sites are more likely as a death is more likely to occur whenever moving individuals come into contact with one another. This drives the population size down. We observe that as the competition rate increases, the fixation probability turns and starts to increase, eventually converges to 0.5. This implies that the entire resident population prior to a mutant arising is converging to 1. When comparing between networks, the fixation probability in the star network turns first and converges faster to 0.5. This is because individuals are more likely to meet in the center site in a star network which drives the population size down faster than the complete and star networks.

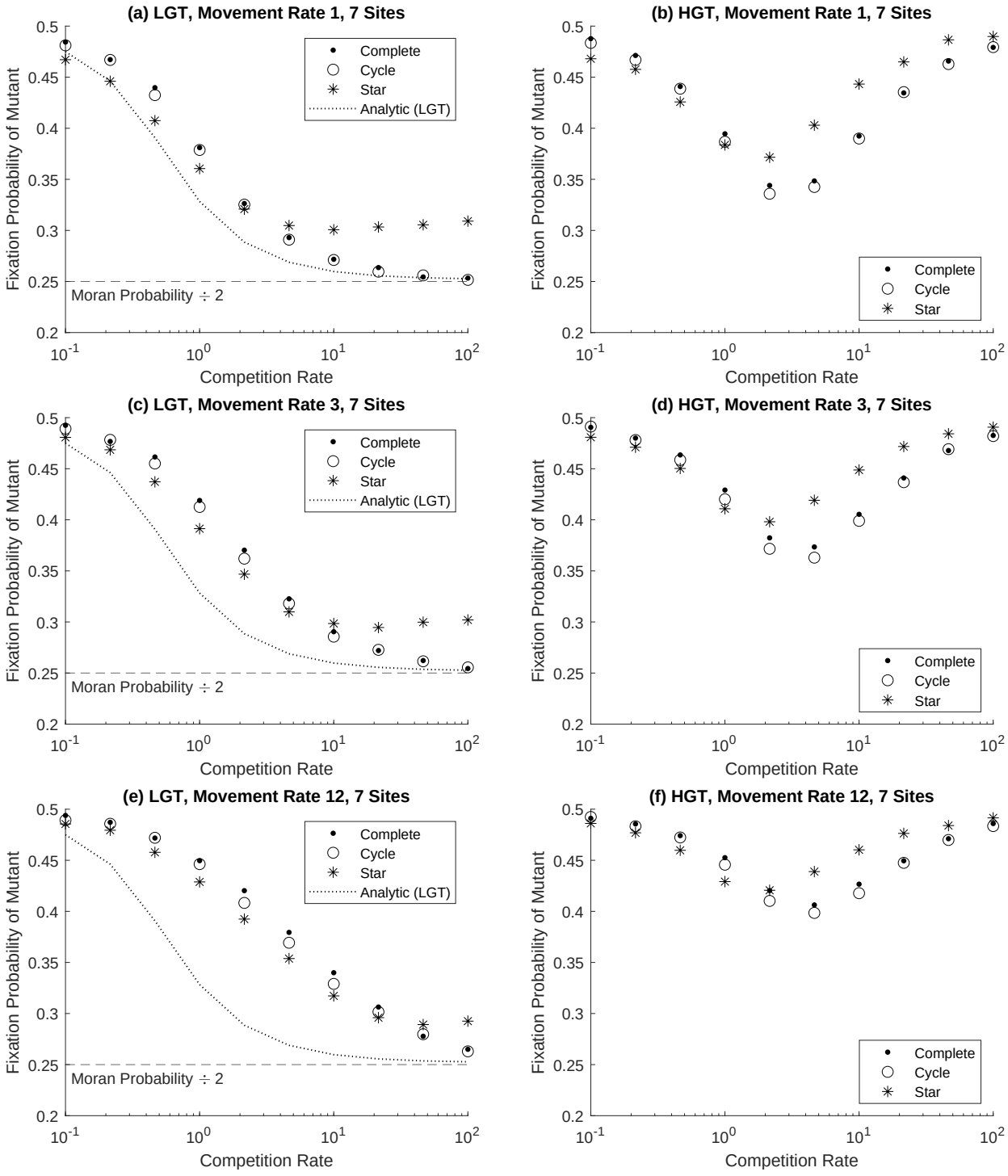

Figure 5: Fixation probability plotted against the competition rate γ for the cycle, complete and star networks. Figures (a) and (c) have low group tolerance, and the dotted line represents a proxy to explain the behaviour observed in Circulation networks (complete and cycle). Figures (b) and (d) have high group tolerance.

6 Discussion

This paper looks at the effect of network structure on mutant invasion, measured in terms of its fixation probability, in a population of variable size. The advantage of allowing variable population size is it allows taking into account change in the distribution of individuals due to different ecological factors. The ones considered here are competition and migration, which allows us to interpret the success of mutant invasion in these terms. The effect of network structure is maximised when competition is high and migration is low, conditional on all sites being occupied by at least one individual. If individuals move unconditionally, the effect of network structure is maximised for intermediate competition rates.

In the case of fixed metapopulations on networks, it was shown by Yagoobi & Traulsen (2021) that the fixation probability in circulation networks is the same regardless of the migration rate. We have shown that for variable metapopulations on networks the fixation probability in circulations networks is identical in the low migration limit. As the migration rate increases this is no longer the case, however, circulation networks still follow each other closely in terms of the fixation probability. This means that circulation networks still have similar qualitative behaviour in terms of the fixation probability in the low mutation limit.

In evolutionary graph theory (Lieberman et al. 2005) and its various extensions Broom et al. (2015), Pattni et al. (2017), Yagoobi & Traulsen (2021) the dynamics of a mutant appearing are left out for simplicity. It is however acknowledged that this can have an effect and are account for, for example, using a temperature weighted fixation probability (Allen & Tarnita 2014). This accounts for where a mutant is likely to appear, instead of assuming that a mutant has a uniform chance of appearing anywhere on a network. A mutant then replaces a resident individual in the population according to the mutant appearance distribution chosen. Whilst this approach was has been previously implemented for variable population sizes (Pattni et al. 2021), it is not representative in general. To obtain a case that is representative, the dynamics of a mutant appearing are taken into account in the model. This means that there is no ambiguity with regards to the mutant appearance distribution as it is determined by the model parameters chosen. It is therefore easier to follow the effect of the mutant appearance distribution with changing model parameters. For example, the star network naturally switches from an amplifier to suppressor of selection as the migration rate increases because of a change in the distribution of individuals across the networks.

The migration regime used here depends upon group preference similar to the implementation in Pattni et al. (2017). Two extreme alternatives were investigated, low group tolerance where individuals migrate only if there is a negative cost associated with the group they are in, and high group tolerance where individuals have no group preference. There is therefore further

scope for studying social dilemmas (Broom et al. 2018) for various levels of group tolerance.

Another scope for investigation is site heterogeneity. In Yagoobi & Traulsen (2021), **?** it was shown that have patches with different capacities can increase the fixation probability. Here, this can be interpreted as sites having different levels of competition due to the availability of resources. This would affect the fixation probability as individuals move between sites of low and high competition.

comaprison to jan work (just found paper to do).

References

Allen, B. & Tarnita, C. E. (2014), 'Measures of success in a class of evolutionary models with fixed population size and structure', *Journal of mathematical biology* **68**(1-2), 109–143.

Broom, M., Lafaye, C., Pattni, K. & Rychtář, J. (2015), 'A study of the dynamics of multi-player games on small networks using territorial interactions', *Journal of Mathematical Biology* **71**(6-7), 1551–1574.

Broom, M., Pattni, K. & Rychtář, J. (2018), 'Generalized Social Dilemmas: The Evolution of Cooperation in Populations with Variable Group Size', *Bulletin of Mathematical Biology* .

Broom, M. & Rychtář, J. (2008), 'An analysis of the fixation probability of a mutant on special classes of non-directed graphs', *Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences* **464**(2098), 2609–2627.

Champagnat, N., Ferrière, R. & Méléard, S. (2006), 'Unifying evolutionary dynamics: From individual stochastic processes to macroscopic models', *Theoretical Population Biology* **69**(3), 297–321.

Hindersin, L. & Traulsen, A. (2015), 'Most Undirected Random Graphs Are Amplifiers of Selection for Birth-Death Dynamics, but Suppressors of Selection for Death-Birth Dynamics', *PLOS Computational Biology* **11**(11), e1004437.

Kaveh, K., Komarova, N. L. & Kohandel, M. (2015), 'The duality of spatial death–birth and birth–death processes and limitations of the isothermal theorem', *Royal Society open science* **2**(4), 140465.

Lieberman, E., Hauert, C. & Nowak, M. (2005), 'Evolutionary dynamics on graphs', *Nature* **433**(7023), 312–316.

Pattni, K., Broom, M. & Rychtář, J. (2017), 'Evolutionary dynamics and the evolution of multiplayer cooperation in a subdivided population', *Journal of Theoretical Biology* **429**, 105–115.

Pattni, K., Broom, M. & Rychtář, J. (2018), 'Evolving multiplayer networks: Modelling the evolution of cooperation in a mobile population', *Discrete & Continuous Dynamical Systems-B* **23**(5), 1975–2004.

Pattni, K., Overton, C. E. & Sharkey, K. J. (2021), 'Evolutionary graph theory derived from eco-evolutionary dynamics', *Journal of Theoretical Biology* **519**, 110648.

Yagoobi, S. & Traulsen, A. (2021), 'Fixation probabilities in network structured meta-populations', *Scientific Reports* **11**(1), 1–9.

7 Appendix

The time when a mutant (individual of type other than resident/Type A) in the population then one can be interested that which type will eventually dominant the population and the other type go extinct. The probability the process will eventually enter a state is called fixation probability. The infinitesimal generator used above give the expected infinitesimal dynamics of functions of continuous-time Markov process. For a function ϕ acting on continuous-time Markov chain $\Gamma(t)$, the infinitesimal generator, $\mathcal{L}$, is defined as

$$\mathcal{L}\phi(\mathcal{S}) = \lim_{t\to 0} \frac{\mathbb{E}[\phi(\Gamma(t))|\Gamma(0) = \mathcal{S}] - \phi(\mathcal{S})}{t}. \tag{26}$$

Let we are interested in finding the hitting probability of the state $\mathcal{A}$ given that the initial state of the population is $\mathcal{S}$, denoted by $h_{\mathcal{A}}$, is given by

$$h_{\mathcal{A}}(\mathcal{S}) = \Pr(T^{\mathcal{A}} < \infty|\Gamma(0) = \mathcal{S}). \tag{27}$$

where $T^{\mathcal{A}}$ is the time when the process first enters state $\mathcal{A}$. The generator defined in Equation 26 for $\phi = h_{\mathcal{A}}$ is written as

$$\mathcal{L}h_{\mathcal{A}}(\mathcal{S}) = \lim_{t\to 0} \frac{\mathbb{E}[h_{\mathcal{A}}(\Gamma(t))|\Gamma(0) = \mathcal{S}] - h_{\mathcal{A}}(\mathcal{S})}{t}. \tag{28}$$

Since $\Gamma(t)$ is Markov chain which starts at $\mathcal{S}$, the process is independent of the history, the expected value of the hitting probability at $t = 0$ and any other time will the same. Therefor, the numerator on the right hand side will be equal to zero. That is,

$$\mathcal{L}h_{\mathcal{A}}(\mathcal{S}) = 0. \tag{29}$$

If the initial and hitting state are the same then then the hitting probability will be 1, i.e $h_{\mathcal{A}}(\mathcal{A}) = 1$. We can say that the hitting probability is given as the minimal non-negative solution of

7.1 bD Evolutionary Graph Theory Dynamics

In evolutionary graph theory (EGT), birth and death are coupled, which means that the population size is fixed. In Pattni et al. (2021), it was shown that EGT dynamics can be obtained from uncoupled birth and death dynamics by considering a limiting case where birth and death are virtually coupled. However, it was stated that bD EGT dynamics could not be obtained because birth and movement were coupled. In bD evolutionary dynamics an individual is randomly chosen for birth who then replaces an individual who is selected inversely proportional to

their fitness, which is a measure of their fecundity. To obtain bD EGT dynamics it is required that birth and movement is not coupled, which is what we have in the birth-death-migration model, as this allows us to consider a limiting case where an individual is chosen for birth independent of movement and death. For example, for low group tolerence the limiting case where we have $\gamma_{00} = \gamma_{01} \to \infty$ and $\gamma_{11} = \gamma_{10} \to \infty$ such that $\gamma_{11}/\gamma_{00} = r$ is the relative fitness between mutants and residents gives us bD dynamics. Details are shown in the appendix. WE CAN CONSIDER THE CASE WHERE WE USE NEGATIVE ECOLOGICAL FEEDBACK LOOP, I'LL SEE WHICH ONE WORKS BETTER.