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Coexistence times in the Moran process with environmental heterogeneity

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Populations evolve in spatially heterogeneous environments. While a certain trait might bring a fitness advantage in some patch of the environment, a different trait might be advantageous in another patch. Here, we study the Moran birth–death process with two types of individuals in a population stretched across two patches of size N, each patch favouring one of the two types. We show that the long-term fate of such populations crucially depends on the migration rate μ between the patches. To classify the possible fates, we use the distinction between polynomial (short) and exponential (long) timescales. We show that when μ is high then one of the two types fixates on the whole population after a number of steps that is only polynomial in N. By contrast, when μ is low then each type holds majority in the patch where it is favoured for a number of steps that is at least exponential in N. Moreover, we precisely identify the threshold migration rate $\mu^\star$ that separates those two scenarios, thereby exactly delineating the situations that support long-term coexistence of the two types. We also discuss the case of various cycle graphs and we present computer simulations that perfectly match our analytical results.

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1. Introduction

Evolution is a stochastic process that acts on populations of reproducing individuals. Each individual has a fitness that determines its reproductive rate. In the absence of mutation, one individual eventually produces a lineage of offspring that takes over the whole population. This event is called a *fixation*. The key quantities of the evolutionary evolutionary process are the fixation probabilities of the respective individuals and the (expected) time until the fixation happens [1–3].

Population structure is known to substantially affect those quantities, thereby altering the typical fate of a population [4–8]. The effects of various population structures are conveniently studied within the framework of evolutionary graph theory [9,10]. The spatial structure of the population is described by a graph (network) whose nodes correspond to sites. Each site is occupied by a single individual and the edges (possibly weighted) represent migration rates between pairs of sites. The population of asexually reproducing individuals then evolves according to a discrete-time stochastic process called the *Moran birth–death process* [11]. In each step, first (birth) an individual is selected for reproduction with probability proportional to its fitness, and then (death) the offspring migrates to a neighbouring site and replaces its initial occupant. Thus the population size N remains constant. The case of a perfectly well-mixed population consisting of N individuals is recovered by taking a complete graph K_N with all edges having unit weight.

Of special interest is the case of a single beneficial mutant with relative fitness advantage $r > 1$ invading a background population of $N - 1$ indistinguishable residents, each with a fitness 1. For the well-mixed population, the *fixation probability* $\rho(K_N, r)$ of the mutant is equal [9] to $(1 - 1/r)/(1 - 1/r^N)$, which tends to $1 - 1/r$ as $N \to \infty$ and, on average, the process terminates after approximately $(1 + 1/r) \cdot N \log N$ steps [12,13]. That is, for fixed $r > 1$, the *fixation time* $\mathrm{FT}(K_N, r)$ is proportional to $N \log N$.

An important driving question in the field over the past decade has been the hunt for population structures, so-called *amplifiers of selection*, that enhance the fixation probability of a single beneficial mutant invading a background population of indistinguishable residents, as compared to the well-mixed population [14–20]. A prime example of an amplifier is a Star graph S_N consisting of $N - 1$ leaf nodes, all of them connected to a single central node (but not to each other). It is known that, in the limit $N \to \infty$, we have [21–23] $\rho(S_N, r) \to 1 - 1/r^2$. When $r = 1 + s$ for s small, this is roughly a twofold increase compared to the baseline given by $\rho(K_N, r)$. Even more strongly, there exist structures (so-called *superamplifiers*) that guarantee fixation of the mutant in the limit $N \to \infty$, no matter how small its fitness advantage $r > 1$ is [24–27].

Regarding the timescale of the process, formal results concerning the Moran birth–death process on structured populations are comparably scarcer and those that exist focus on identifying population structure with short evolutionary timescales. The reason is that such structures, especially when they amplify, could potentially speed up the rate of evolution. For example, it is known that for Star graphs, the process terminates after roughly $N^2 \log N$ steps [28]. More generally, when the underlying graph is undirected (that is, all edges are two-way) then the process terminates after a number of steps that is polynomial in N [29,30]. The trade-off between fixation probability and fixation time has also been studied [31,32]. In particular, it has been established that there exist superamplifiers with short fixation time scales [33]. Moreover, the fixation time has been studied in other models, such as the heterogeneous voter models [34]. However, an important limitation of fixation time as a quantity is that it relates only to the overall duration of the process. In other words, it is oblivious to what is actually happening during the process before one of the types fixates.

More recently, the framework of evolutionary graph theory has been enriched with environmental heterogeneity [35,36]. This is conveniently done by partitioning the sites into patches. The fitness of each individual is constant within each patch but it can vary across different patches, see figure 1b. (We note that, alternatively, following the fundamental work of Sinai [37],
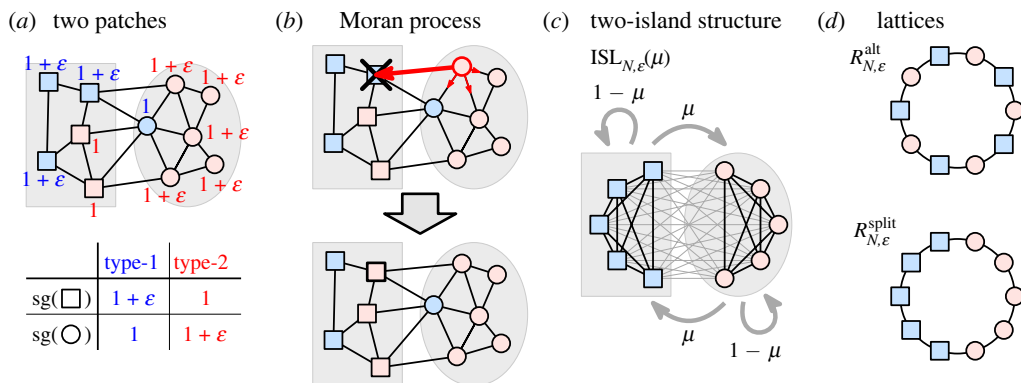
Figure 1. Moran process on a population structure. (*a*) In the population structure, the 2*N* nodes (sites) are split into two patches of size *N* (boxes, circles), each patch giving a relative fitness advantage $1 + \varepsilon$ to one of two possible types of individuals (blue, red, respectively). (*b*) In each step of the Moran process, first an individual is selected for reproduction proportionally to its fitness, and then the offspring replaces a random neighbour. (*c*) In the two-island structure $\mathrm{ISL}_{N,\varepsilon}(\mu)$, each patch is a well-mixed population (island) and the offspring migrates to the other island with probability μ. (*d*) We also consider the one-dimensional lattice, and two special decompositions of its nodes into patches: the nodes either alternate ($R_{N,\varepsilon}^{\mathrm{alt}}$), or they form two large blocks of *N* consecutive nodes ($R_{N,\varepsilon}^{\mathrm{split}}$).

there is a line of research studying the case when the environment itself is random [38,39].) Concerning the fixation probability, analytical results are known for large well-mixed populations with any number of patches [40], and for certain special families of regular graphs with two patches [41]. Concerning the duration of the process, to our knowledge no analytical results are known.

In this work, we study the timescale of the Moran birth–death process in populations that are spatially structured and environmentally heterogeneous. This differs from the earlier research focus in four regards. First, for populations that are environmentally heterogeneous, to our knowledge no analytical results on evolutionary timescales are known (the previous research focused on fixation probabilities of the respective types). Second, for homogeneous populations, the past work related to the duration of the process has focused on identifying population structures with short fixation times (and high fixation probability), since such structures could potentially be used to speed up the evolutionary process. By contrast, our goal here is to characterize structures that support long-term coexistence of the two competing types. Such structures are important in population genetics where they correspond to multiple-niche ecosystems with protected polymorphism [42,43]. As another application, consider single-species biofilms: although very small in scale, biofilms typically consist of several microenvironments and show substantial heterogeneity, both genetic and phenotypic, over considerable time scales [44,45]. In those settings, quantifying the duration of coexistence is more relevant than quantifying the fixation probabilities of the respective types. For example, coexistence and polymorphism have been shown to be relevant in antibiotic drug resistance [46] and drug-gradient *in vitro* models [47]. Third, while the past research used the notion of a fixation time, here we introduce a refined notion of a coexistence time. Our results thus provide stronger guarantees about the state of the population throughout the process. Fourth, we use a distinction between polynomial (short) and exponential (long) timescales. As an illustration, consider a population of size $N = 100$, a polynomial function N^2 and an exponential function 2^N. Then $N^2 = 10^4$ steps correspond to 100 generations, which is a moderate number. By contrast, $2^N \approx 10^{30}$ steps correspond to 10^{28} generations which is effectively infinite for all practical purposes. As a consequence, when evolutionary timescales are exponential, quantities such as fixation probability are largely irrelevant.

In order to present our results, we define a certain natural two-patch population structure $\mathrm{ISL}_{N,\varepsilon}(\mu)$ that corresponds to an island model [48,49] with two islands of equal size N and a bi-directional migration rate μ. Formally, it is defined by three numbers N, ε, μ as follows: two types of individuals are spread over two well-mixed patches of size N each, thus the total population size is $2 \cdot N$. Each type of individual is favoured in one patch, by having relative fitness advantage $1 + \varepsilon$ rather than 1, for some fixed $\varepsilon > 0$. Finally, whenever an individual reproduces, its offspring migrates to the other patch with probability μ and replaces a random individual there (otherwise it replaces a random individual within its patch). Note that this is related to (but different from) the classical source-sink models in population genetics [50].

Here, we present two results on coexistence times of environmentally heterogeneous populations. First, we show that on well-mixed populations, the process terminates after a number of steps that is of the order of at least N^2 and at most N^3. When compared to the $N \log N$ steps on homogeneous well-mixed populations, the process is thus slowed down but the expected number of steps is still only polynomial. Second, we show that the long-term evolution of a Moran birth–death process on the two-island population structure $\mathrm{ISL}_{N,\varepsilon}(\mu)$ crucially depends on the migration rate μ between the two patches. Specifically, we show that when $\mu \geq 1/2$, with high probability, the stochastic process terminates after a number of steps that is only polynomial in N, regardless of $\varepsilon > 0$. Thus, the fixation time is also only polynomial in N. In sharp contrast, when $\mu < 1/2$, with high probability, each type constitutes a majority in the patch where it is favoured for a number of steps that is at least exponential in N. Thus, the fixation time is also at least exponential in N. When combined, those two results present a strong dichotomy and precisely delineate the scenarios that support long-term coexistence of the two types. Those analytical results are particularly relevant in the biological settings mentioned above, where long-term coexistence is important. We also discuss the case of cycle graphs and we present computer simulations that perfectly match our analytical results.

2. Model

We consider the Moran birth–death process acting on structured populations consisting of two types of individuals, T_1 and T_2. First, we recall the general framework of evolutionary graph theory [9], including the environmental heterogeneity [35].

(a) Spatial structure

The spatial structure of a population is described by a connected graph (network) $G = (V, E)$ whose nodes $u \in V$ correspond to sites. Each site is occupied by a single individual and the edges $(u, v) \in E$ (including self-loops) represent where an individual can place an offspring. Moreover, each edge $(u, v) \in E$ is assigned a weight $w_{u,v} \in (0, 1]$ that represents the strength of the connection. The well-mixed population is represented by a complete graph K_N where all edges and self-loops have unit weight.

(b) Environmental heterogeneity

On top of that, each node u is assigned a *signature* $\mathrm{sg}(u) = (f(u)_1, f(u)_2)$, where $f(u)_i$ denotes the fitness of a type T_i individual when it occupies the site u (for $i \in \{1, 2\}$). A set of nodes that all have the same signature is called a *patch*. In this work, we consider populations formed by two patches P_1, P_2, each patch favouring the corresponding type by the same margin ε. In other words, for $u \in P_1$, we have $\mathrm{sg}(u) = (1 + \varepsilon, 1)$, whereas for $u \in P_2$ we have $\mathrm{sg}(u) = (1, 1 + \varepsilon)$, for some fixed $\varepsilon > 0$. See figure 1*a*.

(c) Moran process

The population evolves according to a Moran birth–death process adapted to a population structure. We assume that initially each node in a patch P_i is occupied by an individual of type T_i. The Moran birth–death process is a stochastic (random) process that proceeds in discrete timesteps as follows:

- (i) Birth: select an individual randomly, with probability proportional to its fitness. (That is, denoting the total fitness of the population by F, an individual with fitness f is selected with probability f/F.) That individual, say at node u, produces an offspring which is a copy of itself.
- (ii) death: select a node adjacent to u randomly, with probability proportional to the edge weight $w_{u,v}$. (i.e. a node u' is selected with probability $w_{u,u'}/\sum_{v \in V} w_{u,v}$.) The offspring then migrates to site u' and replaces its original inhabitant.

Note that throughout the process, the population size and structure remain constant. See figure 1*b*.

(d) Fixation time and *c*-coexistence time

When the underlying graph G is connected, the Moran process eventually terminates with one type having spread over all nodes. This event is called *fixation*. For $i \in \{1, 2\}$, we denote by $\rho_i(G)$ the *fixation probability* of type T_i and by FT(G) the *fixation time*, that is, the (expected) number of steps until the process terminates.

Note that the fixation time ignores how the composition of the population fluctuates before the process terminates. To capture those fluctuations, we define a quantity which we call the *coexistence time*. Recall that initially each patch is occupied entirely by the individuals that are favoured in that patch. Intuitively, the coexistence time counts the steps for which each type maintains a majority in its patch. Formally, given a graph G the coexistence time, denoted CT(G), is the expected number of steps until the first moment in time when one of the two types occupies less than one-half of the nodes in its patch. By definition, a coexistence time can never be longer than a fixation time, but it can be substantially shorter. When the coexistence time is long, it means that for a long time each patch is occupied mostly by the individuals that are favoured there. Somewhat more generally, given a constant $c \in (0, 1)$, we define CT$^c(G)$ to be the expected number of steps until the first moment in time when one of the two types occupies less than a fraction of c of its patch. Then for any $c \leq 1/2$, we have CT$^c(G) \geq$ CT$^{1/2}(G) =$ CT(G).

(e) Population structures $\mathrm{ISL}_{N,\varepsilon}(\mu)$, $R_{N,\varepsilon}^{\mathrm{alt}}$, $R_{N,\varepsilon}^{\mathrm{split}}$

Our main results apply to certain two-patch population structures $\mathrm{ISL}_{N,\varepsilon}(\mu)$ characterized by three parameters N, $\varepsilon > 0$, $\mu \in (0, 1)$ as follows: The population structure $\mathrm{ISL}_{N,\varepsilon}(\mu)$ is a complete graph on $2N$ nodes split into two patches P_1, P_2 of size N each. The edges within each patch all have unit weight, the edges connecting nodes in opposite patches all have weight $w = \mu/(1 - \mu)$. This choice of w guarantees that an offspring of a reproducing individual migrates to the opposite patch with probability $Nw/(Nw + N) = \mu$. Finally, each patch increases the fitness of one type from 1 to $1 + \varepsilon$. That is, for $u \in P_1$ we have $\mathrm{sg}(u) = (1 + \varepsilon, 1)$, whereas for $u \in P_2$ we have $\mathrm{sg}(u) = (1, 1 + \varepsilon)$. Specifically, for migration rate $\mu = 1/2$ we recover the case of a well-mixed population $K_{N,\varepsilon}$. See figure 1*c*.

Later, we also study one-dimensional lattices and we investigate how the coexistence time depends on the relative layout of the two patches. The underlying graph is a cycle C_{2N} where the $2N$ nodes are arranged circularly, and each node is connected to its two neighbours by an edge with unit weight. We consider two ways to partition the nodes into patches P_1, P_2: in $R_{N,\varepsilon}^{\mathrm{alt}}$, the nodes alternately belong to P_1 and P_2. In $R_{N,\varepsilon}^{\mathrm{split}}$, both P_1 and P_2 consist of a chunk of N consecutive nodes. See figure 1*d*.

(f) Asymptotic notation

In order to compare the relative growth rate of fixation and coexistence times in the limit of large population size $N \to \infty$, we briefly recall a standard mathematical notation $\Theta(\cdot)$, $\mathcal{O}(\cdot)$ and $\Omega(\cdot)$ for asymptotic tight bound, upper bound and lower bound, respectively. For example, we write $\frac{1}{2}N(N+1) \in \Theta(N^2)$ and $N^2 \in \mathcal{O}(N^3)$ and $2^N \in \Omega(N^3)$ to denote that, up to constant factors, for large N, we have $\frac{1}{2}N(N+1) \approx N^2 \ll N^3 \ll 2^N$. Moreover, we say that a function $f(N)$ is (at most) *polynomial* if $f(N) \in N^{\mathcal{O}(1)}$ and it is (at least) *exponential* if $f(N) \in 2^{\Omega(N)}$. For detailed treatment, see [51, Section 1.3]. We note that the distinction between polynomial and exponential growth rate is fundamental. For example, problems in computer science whose solution can be found in polynomial time are considered tractable in practice, whereas problems requiring exponential time are considered intractable. As mentioned before, exponential timescales are effectively infinite. As an example, even for $N = 100$ the number $2^N \doteq 1.3 \times 10^{30}$ is much larger than the roughly 4×10^{20} milliseconds that passed since the Big Bang.

3. Results

Here, we state our analytical results, give intuition about their proofs, and illustrate them with numerical computations and computer simulations. The fully rigorous mathematical proofs are deferred to electronic supplementary material.

Recall that in all instances, we consider populations of $2N$ individuals split into two patches P_1, P_2 of size N each, each patch increasing the fitness of the respective type of individual from 1 to $1 + \varepsilon$, for some fixed $\varepsilon > 0$.

Our contribution is twofold: first, we analyse the process on three different types of natural population structures, namely the well-mixed populations, the two-island graphs, and different one-dimensional lattices. Later, we prove a general upper bound on the timescale of coexistence.

(a) Complete graphs

First, we consider the case of a well-mixed population $K_{N,\varepsilon}$ spanning two different patches of size N each. Formally, $K_{N,\varepsilon}$ is recovered from the two-island population structure $\mathrm{ISL}_{N,\varepsilon}(\mu)$ by setting the migration rate equal to $\mu = 1/2$.

Theorem 3.1 (Well-mixed populations). *Fix $\varepsilon > 0$. Then*

$$\mathrm{FT}(K_{N,\varepsilon}) \in \Omega(N^2) \quad and \quad \mathrm{FT}(K_{N,\varepsilon}) \in \mathcal{O}(N^3).$$

It is known that in the environmentally homogeneous regime where one type has fitness advantage $1 + \varepsilon$ at all nodes, the fixation time on a well-mixed population is of the order of $\Theta(N \log N)$ steps [12,13]. The asymptotic lower bound $\mathrm{FT}(K_{N,\varepsilon}) \in \Omega(N^2)$ in theorem 3.1 thus implies that with environmental heterogeneity, the fixation time is increased. However, the asymptotic upper bound $\mathrm{FT}(K_{N,\varepsilon}) \in \mathcal{O}(N^3)$ implies that the process still terminates after a number of steps that is only polynomial in the population size (namely at most cubic), and thus long-term coexistence is not supported. Numerical computation suggests that for any $\varepsilon > 0$ the fixation time in fact scales as $\Theta(N^2)$, see figure 2*a*.

The idea behind the proof is as follows: we represent the stochastic process as a Markov chain that has a state for every possible configuration of mutants and residents. We then define a carefully chosen 'potential function' that assigns a real number to each possible configuration and we prove that, in each step of the process, this potential function changes in a controlled way, in expectation. Namely, we prove that it increases at most by δ_1 and at least by δ_2, where $\delta_1 > \delta_2 > 0$ are two real constants. Since we can also compute the initial and the final value of this potential function, this allows us to bound the expected number of steps that happen until fixation occurs. See electronic supplementary material for a full proof.
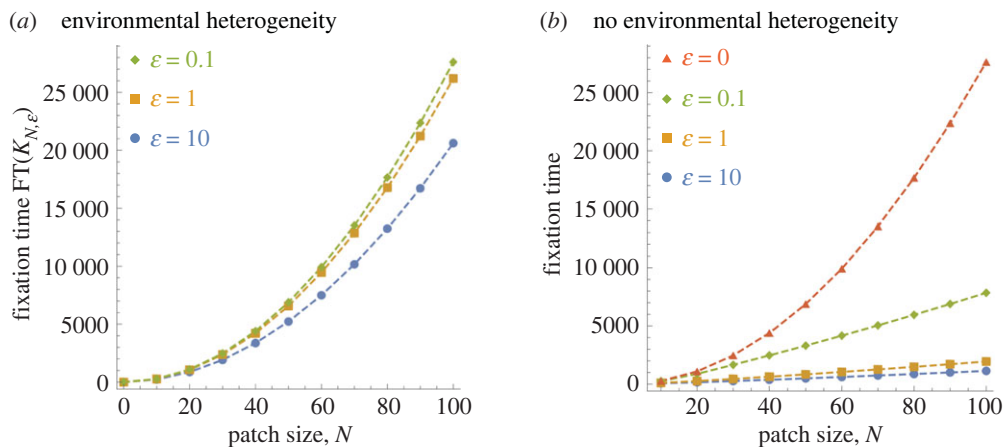
Figure 2. Fixation time on a complete graph $K_{N,\varepsilon}$. (*a*) Numerical computation shows that for a fixed $\varepsilon > 0$ the fixation time $FT(K_{N,\varepsilon})$ scales as $c_\varepsilon \cdot N^2$. Thus the lower bound $FT(K_{N,\varepsilon}) \in \Omega(N^2)$ from theorem 3.1 is tight. Specifically, we obtain $c_{10} \doteq 2.07$, $c_{0.1} \doteq 2.62$ and $c_{0.01} \doteq 2.76$. (*b*) In the regime without environmental heterogeneity (that is, when the same type is favoured in both patches), the fixation time is known to scale as $\Theta(N \log N)$ when $\varepsilon > 0$ and as $\Theta(N^2)$ when $\varepsilon = 0$. Here, $N = 10, 20, \ldots, 100$.

(b) Two-island graphs

Second, we show that for the two-island population structure $ISL_{N,\varepsilon}(\mu)$, the migration rate $\mu^\star = 1/2$ which corresponds to the well-mixed population is in fact a threshold value. Recall that for a given population structure G_N, the quantity $CT(G_N)$ is the (expected) number of steps until either of the types ceases to hold a majority in the patch where it is favoured.

Theorem 3.2 (High migration rate). *Fix $\varepsilon > 0$ and $\mu \geq 1/2$. Then $FT(ISL_{N,\varepsilon}(\mu)) \in \mathcal{O}(N^3)$.*

Theorem 3.3 (Low migration rate). *Fix $\varepsilon > 0$ and $\mu < 1/2$. Then $CT(ISL_{N,\varepsilon}(\mu)) \in 2^{\Omega(N)}$.*

Theorem 3.2 states that when the migration rate exceeds the threshold value $\mu^\star = 1/2$, or is equal to it, then fixation time is still only polynomial in the population size, thus long-term coexistence is not supported. By contrast, theorem 3.3 shows that for migration rates $\mu < \mu^\star$, each type maintains a majority in the patch where it is favoured for a number of generations that is exponential in the population size, see figure 3.

The proof of theorem 3.2 is an extension of the argument used to derive theorem 3.1. As for the argument behind the proof of theorem 3.3, intuitively the idea is to show that in order for one type to lose majority in the patch where it is favoured, the random evolutionary trajectory would have to cross one of three 'barriers', each with a 'thickness' that is linear in N. Using standard results on the absorption time of one-dimensional random walks with constant forward bias, this allows us to conclude that for a number of steps that is exponential in N, with high probability none of the three barriers will be crossed and thus coexistence will be maintained. See electronic supplementary material for a full proof.

(c) One-dimensional lattices

Third, we show that even if we fix the underlying graph and the effects of the patches on the fitness, the coexistence time critically depends on the relative layout of the two patches. To that end, we consider large one-dimensional lattices $R^{alt}(N, \varepsilon)$ and $R^{split}(N, \varepsilon)$ (see figure 1*d*).

Theorem 3.4 (One-dimensional lattices). *Fix $\varepsilon > 0$. Then*

$$FT(R^{alt}(N, \varepsilon)) \in \mathcal{O}(N^3) \quad and \quad CT(R^{split}(N, \varepsilon)) \in 2^{\Omega(N)}.$$
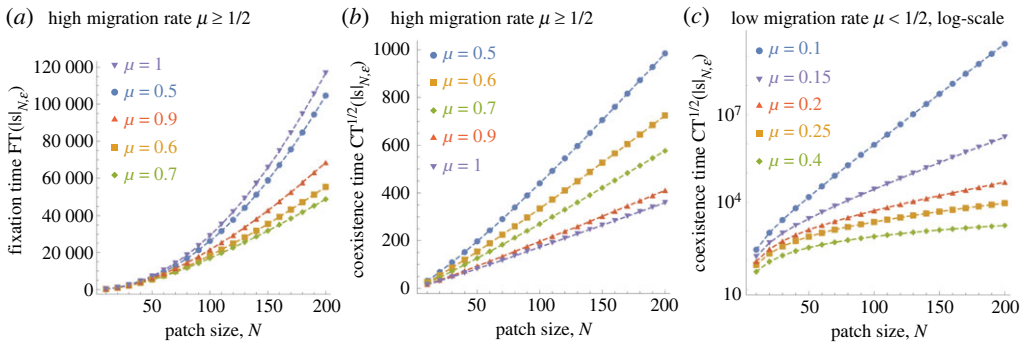
Figure 3. Fixation time on a two-island graph $\mathrm{ISL}_{N,\varepsilon}(\mu)$. (*a*) Numerical computation illustrates that when $\mu \geq 1/2$, the fixation time $\mathrm{FT}(\mathrm{ISL}_{N,\varepsilon}(\mu))$ scales as N^2 (when $\mu = 0.5$ or $\mu = 1$), or even slower than that (when $0.5 < \mu < 1$). This is in agreement with the upper bound $\mathrm{FT}(\mathrm{ISL}_{N,\varepsilon}(\mu)) \in \mathcal{O}(N^3)$ from theorem 3.2. (*b*) The coexistence time $\mathrm{CT}(\mathrm{ISL}_{N,\varepsilon}(\mu))$ is substantially shorter, scaling roughly linearly with the population size N. (*c*) By contrast, when $\mu < 1/2$, the coexistence time $\mathrm{CT}(\mathrm{ISL}_{N,\varepsilon}(\mu))$, and thus also the fixation time, is at least exponential in the population size N (here the y-axis is log-scale). This is in agreement with theorem 3.3. In all panels, we consider $\varepsilon = 1$ and $N = 10, 20, \ldots, 200$.
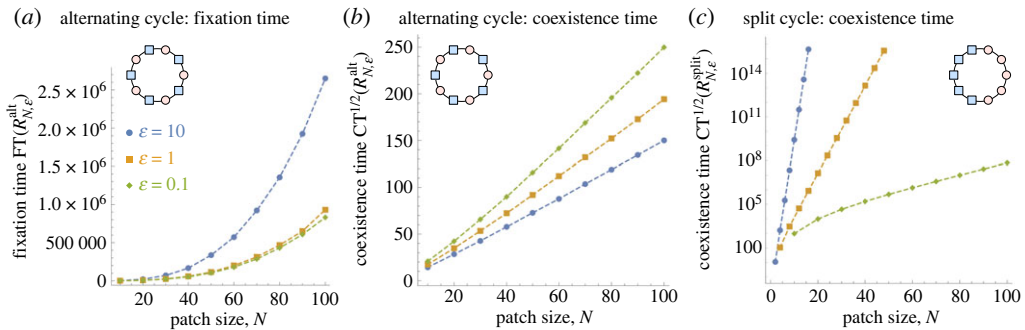

Figure 4. Fixation time on one-dimensional lattices. (*a*) Computer simulations (10^4 repetitions) show that on the Alternating cycle $R^{\mathrm{alt}}(N, \varepsilon)$ the fixation time $\mathrm{FT}(R^{\mathrm{alt}}(N, \varepsilon))$ scales as $\Theta(N^3)$, for any $\varepsilon > 0$. This is in perfect agreement with the upper bound $\mathcal{O}(N^3)$ from theorem 3.4. (*b*) The coexistence time $\mathrm{CT}(R^{\mathrm{alt}}(N, \varepsilon))$ is even shorter—it scales roughly as $\Theta(N)$ for any $\varepsilon > 0$, and curiously it is shorter when ε is larger. (*c*) By contrast, on the Split cycle $R^{\mathrm{split}}(N, \varepsilon)$, the coexistence time $\mathrm{CT}(R^{\mathrm{split}}(N, \varepsilon))$ is exponential in the population size N (note that the y-axis is log-scale). In all panels, we consider $\varepsilon \in \{10, 1, 0.1\}$ and N up to 100.

In other words, when the nodes of a long one-dimensional lattice alternately belong to patches P_1 and P_2 then the process terminates in polynomial time. By contrast, when each patch forms a contiguous block of N nodes, each type holds a majority in its patch for a number of steps that is exponential in N, see figure 4.

The argument behind the first claim makes use of the fact that the evolution on $R^{\mathrm{alt}}(N, \varepsilon)$ can be efficiently mapped to an evolution on a well-mixed population [35,41]. The idea behind the proof of the second claim is that each patch contains a 'core'—a large set of nodes in its middle which is well protected from the invasion by the other type, and which is maintained over an exponential timescale. See electronic supplementary material for a full proof.

(d) General upper bound

Finally, we show that within a certain broad class of population structures, a coexistence on a substantially longer than exponential timescale is impossible. Thus the exponential coexistence

that occurs for two-island structures with low migration rates and for certain one-dimensional lattices is close to optimal. Namely, given a real number $w_{\min} > 0$ we denote by $\mathcal{G}(w_{\min})$ the class of all connected graphs in which each edge, if it exists between two nodes, is assigned a weight at least $w_{\min}$.

Theorem 3.5 (General upper bound). *Fix $w_{\min} > 0$ and $\varepsilon > 0$. Then for any population structure $G_{N,\varepsilon} \in \mathcal{G}(w_{\min})$ on 2N nodes we have $FT(G_{N,\varepsilon}) \in 2^{\mathcal{O}(N \cdot \log N)}$.*

Note that theorem 3.5 gives an upper bound on the fixation time, and thus also on the c-coexistence time for any $c > 0$. The proof is based on a simple idea that if, from any configuration of individuals, a fixation occurs with probability at least p_{fix} within the next s steps, then the fixation time is at most s/p_{fix}. Moreover, the statement applies more generally to any number of patches of arbitrary sizes and with arbitrary (but fixed) signatures. See electronic supplementary material for a full proof.

4. Conclusion

In this work, we used the framework of evolutionary graph theory to study the evolutionary timescales of populations that are both spatially structured and environmentally heterogeneous. To our knowledge, the previous research in this setting focused either on computing the fixation probabilities, or on identifying population structures with short evolutionary timescales. By contrast, our main focus here was to characterize structures that support long-term coexistence of two competing types.

To that end, we considered the Moran birth–death process acting on populations stretched across two patches, where each of the two competing types has a fixed selective advantage in one patch. To address the question of long-term coexistence of the two types, we refined the classical notion of a fixation time and defined the coexistence time as the (expected) number of steps during which each type constitutes a majority in the patch where it is favoured. For certain natural two-island population structures characterized by a migration rate μ, we then showed that the long-term behaviour of the system exhibits a threshold behaviour in parameter μ: when the migration rate is high ($\mu \geq 1/2$), the process terminates with one type fixating on the whole population after a number of steps that is only polynomial in the population size N. In sharp contrast, when the migration rate is low ($\mu < 1/2$), the two types coexist for a number of steps that is (at least) exponential in N. We also showed that on a fixed population structure given by a one-dimensional lattice, the coexistence time can be both polynomial and exponential, depending on the relative layout of the two patches. We note that for random environments, the fundamental result is due to Sinai [37].

Coexistence of multiple types of individuals in structured populations has been extensively studied in various fields [52–55]. Below we list some results for related models, highlighting the differences to our setup. In the terminology of population genetics, the analogue of our question is whether polymorphism is protected in a one-locus, two-allele population inhabiting a two-niche ecosystem. Following the seminal work of Levene [42], a now classic line of research identified several necessary and sufficient conditions for the polymorphism to be maintained [56–62]. However, those results are derived for deterministic models under the assumption of infinite population size, see also [63,64] for reviews. By contrast, our model accounts for stochasticity inherent to the evolutionary process [65], it deals with populations of finite (and arbitrarily large) size, and it classifies the fate of the population in terms of the polynomial-exponential dichotomy. In statistical physics, similar models are studied under the name of interacting particle systems [66]. Those models are stochastic and spatial but the spatial structure is typically assumed to be an integer lattice. Again, conditions characterizing coexistence are known [67,68].

The most closely related results to ours are those that study stochastic models on spatial structures that correspond to island models of finite size. As with the simpler regime without any environmental heterogeneity, fixation probability is a quantity that is relatively approachable

[69–72]. Regarding fixation time, building on the work of Bulmer [73], Yeaman & Otto [74] use computer simulations to observe that polymorphism is maintained when the migration rate exceeds a certain critical threshold and they approximate the threshold by splicing the predictions of the deterministic models with a diffusion approximation for finite populations. While their results are qualitatively similar to ours, there are important differences. First, we work with a purely stochastic model and we directly analyse the underlying Markov chain which allows us to obtain exact rigorous mathematical results without resorting to heuristic arguments. Second, we highlight the fundamental distinction between polynomial and exponential timescales.

Within the field of evolutionary graph theory, the past research agenda related to the evolutionary timescale focused mostly on understanding which population structures lead to short timescales. Here, our objective is the exact opposite—we study population structures that lead to long evolutionary timescales. Furthermore, using the refined notion of a coexistence time (rather than simply a fixation time) we are able to guarantee that not only will the evolutionary process run for exponentially many steps, but also that throughout that timeframe each type will constitute a healthy portion of the population.

At first glance, our results indicate that population structures that are more conducive to long-term coexistence are those in which there is a positive correlation between the environment seen by a parent and its offspring. That is, based on our results it is natural to expect long-term coexistence when the offspring is fairly likely to stay in the same patch as the parent, and to expect only short-term coexistence when the offspring is likely to migrate to the other patch. While this is perfectly true for the two-island population structure (the migration threshold being precisely $\mu = 1/2$), in the next two examples, we show that in general this is only a rule of thumb.

As the first example, consider a large cycle graph where the two patches form alternating blocks of fixed length 4. The probability that an offspring stays in the same patch is then 3/4, but computer simulations analogous to those in figure 4 show that the coexistence time scales only polynomially. To understand this intuitively, suppose that each type of individual occupies one long contiguous segment, and consider the boundary between them. If the boundary occurs within a patch P_1 then the type-1 individuals have a constant-factor advantage to push the boundary by one position, and vice versa. Since the blocks have constant length and alternate regularly, the evolutionary landscape is 'flat' and the coexistence time (as well as the fixation time) are short, that is, polynomial.

By contrast, as another example consider a large one-dimensional lattice where each node belongs to a patch selected uniformly at random, independently of other nodes. The probability that an offspring stays in the same patch is then 1/2. However, most of those structures support long-term coexistence. Indeed, as shown by Sinai [37], for most such structures a boundary between long segments of type-1 and type-2 individuals moves by only roughly $\log^2(n)$ positions in any n steps of the process, thus the fixation time is exponential. In this sense, most one-dimensional lattices behave more like the 'split' graph $R^{split}(N, \varepsilon)$ rather than like the 'alternating' graph $R^{alt}(N, \varepsilon)$.

In this work, we focus on the simple population structures, such as the well-mixed populations, one-dimensional lattices, and two-island populations, in which the roles of the two types are perfectly symmetric. This allows us to cleanly introduce the key notions and derive exact analytical results. To conclude, we briefly discuss several possible extensions and generalizations.

First, throughout this work for simplicity, we focused on c-coexistence time with $c = 1/2$, that is, we postulated that the two types coexist if each type maintains at least $c \cdot |P_i|$ individuals in its patch P_i. We now make two remarks about the case $c \neq 1/2$ in the context of two-island graphs. On one hand, theorem 3.2 shows that when $\mu \geq 1/2$ then the fixation time is polynomial, and so there is no long-term coexistence for any $c \in (0, 1)$. On the other hand, theorem 3.3 shows that if $\mu < 1/2$ then there is long-term coexistence with $c = 1/2$, and therefore obviously also long-term coexistence with any $c' < 1/2$. However, it is not clear whether there is also long-term coexistence with some $c' > 1/2$. Presumably, the highest value of c' for which there is c'-coexistence depends on the parameters μ and ε.

Second, throughout this work, we derived results for two perfectly symmetric types of individuals living on symmetric population structures. Do analogous results hold for asymmetric population structures? Or for symmetric population structures with asymmetric patch patterns? Or for symmetric patch patterns, where each type has a distinct fitness advantage ε_i in its patch? Or for more than two types of individuals? Or for other update mechanisms, such as death–birth updating? It is our hope that a subsequent work on more complex population structures, possibly with multiple asymmetric patches and with multiple competing types, will lead towards a better understanding of the role of diversity and its maintenance in populations at large.

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