Time scales and species coexistence in chaotic flows

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PACS 87.23.Cc – Population dynamics and ecological pattern formation
PACS 05.40.-a – Fluctuation phenomena, random processes, noise, and Brownian motion
PACS 47.54.Fj – Chemical and biological applications
PACS 89.75.Hc – Networks and genealogical trees

Abstract – Models of species coexistence often involve spatial heterogeneity, generated by an interplay of environmental flow and biological dynamics. To characterise this scenario, we consider a finite community of two different species, advected by a chaotic flow. Intrinsic stochasticity eventually leads to the extinction of one species. Contrary to intuition however, varying the relative time scales of population dynamics and flow does not interpolate straightforwardly between the no-flow and well-mixed limits; instead we find long-lasting species coexistence at intermediate Damköhler numbers. Our analysis shows that this slowdown is due to spatial organisation on a modularised network. We also find that diffusion can either slow down or speed up fixation, depending on the relative time scales of flow and population dynamics.

Introduction. Gause’s exclusion principle suggests that two species competing for the same resources cannot coexist in the long term [1,2]. This is at odds with the biodiversity in marine ecosystems [3] and with the idea of coexisting replicators in the prebiotic soup (see e.g. [4]). The exclusion principle is based on the assumption of perfect mixing; models of biodiversity often involve spatial heterogeneity instead, generated by chaotic flows with transport barriers, fractal filaments or other types of imperfect mixing [4–19]. This is supported by satellite observations for example of chlorophyll concentrations off the coast of South America [20,21].

Explanations of species coexistence involving hydrodynamic flow and biological dynamics naturally raise the question of the interplay between the relevant time scales [5]. This is commonly quantified by the Damköhler number, i.e., the ratio between the time scales associated with the flow and the biological (or chemical) processes [5,9–12,22]. In many existing models of biodiversity the biological reaction dynamics is described by deterministic differential equations, neglecting the effects of demographic noise and intrinsic stochasticity. While this may be appropriate for large-scale systems, intrinsic noise is known to be essential for fixation and extinction in finite populations [23,24]. The aim of our work is to address this gap. We use a stylised model combining chaotic flow and stochastic population dynamics to identify long-lasting species coexistence at intermediate Damköhler numbers; the simplicity of the model allows us to characterise the effects leading to this slowdown of extinction.

Each individual in our model belongs to one of two species; these particles are advected by a chaotic flow. Our analysis focuses on the mean time until one species is eliminated, known as the time to fixation [23,24]. In each step of the population dynamics one particle is selected for removal, and a randomly chosen particle in its vicinity reproduces, similar to dynamics of the well-known voter model (VM) [25]. Stylised neutral models of this type have been used in ecology, but also in the context of opinion dynamics and language evolution, for examples see [26,27]. The combination of a finite interaction range and the underlying flow leads to a constantly changing interaction network. Adaptive networks in existing studies of VMs typically evolve through a process of rewiring, driven by the individuals at its nodes [28,29]. In contrast, the network in our model is shaped by the flow. The positions of the particles are not constrained to a discrete lattice, and a heterogeneous network can form, distinguishing our work from that of [8].

Varying the Damköhler number interpolates between...
two extremes: a static network in the limit of infinitely fast population dynamics, and an effectively well-mixed system for very fast flow. Fixation times in simple well-mixed systems can be obtained analytically, and it is well known that fixation in the VM happens much sooner in a well-mixed situation than in static networks [30,31].

Surprisingly, our analysis shows that the interpolation between these regimes is not necessarily monotonic; fixation can be slowest when the time scales of flow and population dynamics balance. This indicates that moderate stirring can maintain species coexistence for longer than complete mixing or the absence of any flow.

Model. The model describes a population of \( N \) individuals in a two-dimensional domain \([0,1]^2\) with periodic boundary conditions. The size of the population is constant. We write \( x_i(t) \) and \( y_i(t) \) for the coordinates of particle \( i \). Each particle can be in one of two states, \( \sigma_i(t) \in \{0,1\} \), representing the species (or type) the individual belongs to. The key components of the model are (i) a flow field advecting the particles, and (ii) the population dynamics. The aim of our work is not to study the detailed effects of different chaotic flows. Instead we choose a periodic parallel shear flow as a simple representative, displaying repeated stretching and folding and mimicking turbulent flow [32–34]. The individuals are treated as Lagrangian particles; we write \( \dot{x}_i = s_1(x_i, y_i, t), \dot{y}_i = s_2(x_i, y_i, t) \), where the quantities \( \dot{x}_i \) and \( \dot{y}_i \) are derivatives with respect to \( t \). During the first half of each period the shear flow is given by

\[
 s_1(x_i, y_i, t) = V_0 \sin[2\pi y_i + \phi], \quad s_2(x_i, y_i, t) = 0. \tag{1}
\]

We choose a period of one, \( V_0 \) sets the flow velocity. During the second half of each period one has

\[
 s_1(x_i, y_i, t) = 0, \quad s_2(x_i, y_i, t) = V_0 \sin[2\pi x_i + \phi]. \tag{2}
\]

The phase \( \phi \) is drawn at random from a uniform distribution over \([0,2\pi]\) for each period. These equations of motion are integrated by standard methods. We compare the outcome for this structured flow with that of entirely random diffusion

\[
 \dot{x}_i = \xi_i, \quad \dot{y}_i = \eta_i, \tag{3}
\]

with \( \xi_i, \eta_i \) independent Gaussian processes of mean zero. We also consider interpolations between structured flow and diffusion,

\[
 \dot{x}_i = \sqrt{1 - \alpha^2} s_1 + \alpha \xi_i, \quad 0 \leq \alpha \leq 1, \tag{4}
\]

and similar for \( \dot{y}_i \). The amplitude of the diffusive flow is chosen such that the root-mean-square velocity is constant for all \( \alpha \), i.e., \( \langle \dot{x}_i^2 + \dot{y}_i^2 \rangle^{1/2} = V_0/2 \), with \( \langle \cdot \cdot \rangle \) a spatial average.

Interaction between particles occurs within a radius \( \delta \). For given particle positions this defines an interaction network. Particles reside at the nodes of the graph, and two particles are connected by an edge whenever their Euclidean distance is at most \( \delta \). Writing \( N = n^2 \) is particularly convenient when the initial positions form a regular \( n \times n \) lattice, embedded in the spatial domain \([0,1]^2\). It is then useful to write \( \delta = R/n; R > 0 \) measures the interaction radius in units of lattice spacings. The population dynamics begins at the same time as the flow, and proceeds as follows: in each microscopic step we select one particle, \( i \), at random for removal. Of all particles within radius \( \delta \) around \( i \) one particle \( j \) is selected at random for reproduction. This reflects neutral selection. The offspring is of the same type as its parent, and is placed at position \((x_i, y_i)\). Effectively particle \( i \) has adopted state \( \sigma_j(t) \). This corresponds to the well known voter model [25], albeit on a dynamic network shaped by the flow.

The relative time scales between flow and population dynamics are controlled by the Damköhler number \( Da \). We execute one sweep of \( N \) steps of the population dynamics every \( 1/Da \) units of time, \( t \). The quantity \( Da \) is the average number of reproduction events each particle undergoes per unit time. We write \( \tau = Da t \) for the number of sweeps by \( t \). We note that the parameter \( V_0 \) in Eqs. (1,2) represents an inverse characteristic time scale of the flow.

Except for static networks with several disconnected components, the population dynamics will eventually come to an end when one species has gone extinct. This process occurs through the formation of domains of particles of the same type. These domains gradually coarsen until one domain extends across the entire system; the surviving species has reached fixation. Our main interest is the time it takes to reach this state.

Results. Our principal result is shown in the main panel of Fig. 1. Starting from a regular grid we have measured
the time to fixation, \( \tau_{C} \), as a function of the Damköhler number. Consistent with the intuitive expectation the limits of small and large Damköhler numbers reproduce results for the well-mixed and no-flow cases respectively

\[
(\tau_{C}/N \approx \ln 2 \text{ for the well-mixed system}) \quad \text{and} \quad \tau_{C}/N \approx 1.19
\]

from simulations on a static \( 30 \times 30 \) lattice, \( R = 1.5 \). Intriguingly, however the interpolation between these limits is not monotonic; we observe a maximum in time to fixation at intermediate Damköhler number. While we report data for \( 30 \times 30 \) particles in the figure, we have tested larger particle numbers as well, with similar results. The maximum is found for the shear and for diffusion; the location of this maximum varies with the interpolation parameter \( \alpha \), as seen in the inset of Fig. 1. It is these observations that we seek to explain in the following.

**Interpretation.** The data for the shear flow in Fig. 1 shows that the time to fixation is that of the no-flow case for high Damköhler numbers, \( Da > Da_{c} \). The following order-of-magnitude calculation helps to develop physical insight. We first present the general argument and then verify this using the specific parameters of our simulations. The network changes independently of the population dynamics, and it is reasonable to assert that no significant departures from the regular grid are seen until a time \( t_{d} \). Moreover, \( \tau_{C}/N \approx 1 \) for all Damköhler numbers. We can then estimate \( Da_{c} \) as the the point at which \( \tau_{C} \approx Da_{c}t_{d} \); for \( Da \geq Da_{c} \) fixation is reached before the shear flow has noticeably distorted the initial grid; the fixation time is that of the VM in a static environment. This is confirmed in Fig. 1, we estimate \( t_{d} \approx 0.01 \) \([35]\); using \( N = 10^{3} \) for the order-of-magnitude calculation then gives \( Da_{c} \approx 10^{5} \), consistent with Fig. 1.

The network evolves indefinitely, but will eventually reach a dynamic stationary state, we denote the time to reach this state by \( t_{s} \). This is the time by which the initial network has been forgotten, and indicates the time scale on which a renewal of the graph occurs. The point of maximal slowdown corresponds to the Damköhler number \( Da^{*} \) at which the time scale of network renewal is of the same order as the consensus time, \( \tau_{C} \approx Da^{*}t_{s} \).

We have tested this for the simulations shown in Fig. 1. Specifically, we estimate \( t_{s} \approx 5 \) from measuring the half-life of links in the network \([35]\). The dot-dashed line in Fig. 1 indicates \( t_{s} = Da_{c}t_{s} \). As seen in the figure \( t_{s} \approx \tau_{C} \) at the point of maximal slowdown. Using \( \tau_{C}/N \approx 1 \) as before and \( t_{s} = 10 \) for an order-of-magnitude estimate we find \( Da^{*} \approx 10^{2} \) as the point at which population dynamics and network renewal occur on the same time scale, consistent with the location of the maximum.

The following physical picture emerges. At very slow flow, \( Da > Da_{c} \), the population dynamics effectively occurs on the network set by the initial condition. At Damköhler numbers just below \( Da_{c} \) the coarsening dynamics occurs on a slowly changing network, with only minor distortions from the initial grid, see Fig. 2(a). For an example. For \( Da^{*} \lesssim Da \lesssim Da_{c} \) the population dynamics proceeds adiabatically on a changing network, advected by the flow from the initial grid towards more disorder. This leads to a slowdown of fixation. As a control experiment we have simulated the VM on the largest connected component of static networks obtained by applying random displacements of the order of the lattice spacing to the nodes of the grid. This disorder increases the time to fixation. The reason for this slowdown is a spatial organisation on an increasingly modularised network. For the advected case this can be seen in Fig. 2(b); patches of particles of the same type are found, broadly corresponding to highly-connected modules of the network. Coarsening occurs at the interfaces of domains, and the relatively low connectivity between patches hinders fixation.

To quantify this spatial organisation we measure the fraction \( m \) of type-1 particles in the system and the probability that a randomly chosen link connects two particles of opposite types, i.e., the fraction of active links, \( \rho_{a} \). We then compute

\[
\rho = \frac{\rho_{a}}{2m(1-m)}.
\]

The denominator is known as the heterozygosity \([16]\), and represents the probability that two individuals chosen at random without regard of the network are of opposite
types. Fig. 3(a) shows that the order parameter $\rho$ initially decreases as spatial domains form. It reaches a plateau before fixation; the numerical value of $\rho$ at the plateau is an indicator of the spatial organisation in this quasi-stationary state. In absence of any spatial correlation one would find $\rho = 1$; smaller values indicate clustering of particles of the same type on neighbouring nodes in the network, as shown in Fig. 2(b). We stress that this notion of clustering refers to the organisation of the species on the network, but not to potential clustering of the nodes in space. As seen in Fig. 3(b) maximal clustering on the network occurs for intermediate Damköhler numbers, $Da \approx Da^*$. This leads to a lack of active interfaces on the graph, slowing down the coarsening process consistent with the maximum observed for the time to fixation in Fig. 1.

We next discuss the regime of fast flow. For $Da \lesssim Da^*$, the network is no longer quasi-static on the time scale of the population dynamics. The graph is still disordered at any one time, but the population cannot organise on the rapidly changing graph. This is seen in Fig. 2(c), where the extinction process has advanced, but where the minority species is scattered across the network. Hence the plateau value of the order parameter $\rho$ is increased (Fig. 3). For very fast stirring the network changes so quickly that particles effectively interact with partners newly sampled at random from the entire population at each step of the biological dynamics. We recover the consensus time of the well mixed VM, see Fig. 1.

**Diffusion.** For purely diffusive motion equilibration of the network occurs at $t_\rho \approx 0.01$ in our simulations. This indicates a speed-up of network turnover compared to the structured flow, as intuitively expected. The shear flow is relatively coherent and parallel to the axes. In diffusion particle movements are uncorrelated, implying faster mixing. Comparing panels (d) and (e) in Fig. 2 against panel (a) demonstrates this: these three snapshots are all taken at $t = 0.02$. In-line with the speed-up the maximum fixation time is found at $Da^* \approx 10^5$ for diffusion, see Fig. 1. The data reveals an interesting effect; adding Brownian noise to the structured flow can accelerate fixation at $Da \approx 10^3 - 10^4$, but leads to a slowdown of fixation at higher Damköhler numbers, $Da \approx 10^4 - 10^6$.

**Role of the initial network.** Focusing on the structured flow we have tested different initial networks, displacing the nodes of a regular grid by random amounts in $[-b, b]$. For $Da \lesssim Da^* \approx 10^2$ the flow is sufficiently fast to wash out the initial condition before the population reaches an absorbing state; as seen in Fig. 4 the fixation time is not affected by the random displacements. For $Da \gtrsim Da^*$, adding disorder to the initial grid increases the fixation time. A similar effect can be obtained by starting the flow from a regular grid, but initiating the population dynamics only after some transient time. This highlights the role of the flow in generating a modular network. Moderate flow can slow down fixation if the population dynamics starts from an ordered grid. This slowdown is due to the disorder generated by the flow. If the initial graph already contains sufficient disorder the flow does not create any additional modularity. It mainly stirs the nodes resulting in a monotonic reduction of fixation time with increased flow. An interesting numerical experiment can be performed by initially placing all particles inside a ball of diameter $\delta$. This describes the situation of a densely populated colony, and constitutes a well mixed system in the no-flow limit. For very fast flow the system will effectively be well mixed as well. In either of the two limits the fixation time is $\tau_C = N \ln 2$. As seen in Fig. 4 the interpolating behaviour is again non-monotonic, with significant slowdown of fixation at intermediate Damköhler numbers.

**Conclusions.** We have studied the effects of a chaotic flow on the stylised dynamics in a finite population of interacting species. The flow generates a dynamic interac-
tion network, and intrinsic noise in the population eventually leads to fixation of one species. If the initial particle positions form an ordered structure a slowdown of fixation occurs at intermediate Damköhler numbers. Species can coexist the longest when the speed of network turnover is comparable to that of the macroscopic population dynamics. We show that the effect in our model is due to heterogeneity in the interaction network, generated by the flow. Simulations not shown here demonstrate that the effect is not limited to the shear flow or diffusion; we have simulated the dynamics in a double gyre flow [36], and the effect persists. We have also observed a maximum in fixation time at intermediate Damköhler numbers in simulations with inertial particles. These results will be reported elsewhere in more detail. We have also tested a scenario in which an initially dense population is placed into a flowing medium (Fig. 4), and another in which a small group of mutants with a fitness advantage invades a resident population [37]. Results again indicate that species coexist the longest at intermediate Damköhler numbers. These findings suggest that the slowdown effect is robust, and that it may persist in more elaborate models of population dynamics with multiple time scales. We also note that these results are reminiscent of observations in the ecological literature where it was found that maximal diversity is obtained for intermediate levels of dispersal, both in computational models and in experiments on a wide range of organisms [38–42].

**References**

TG would like to thank the Group of Nonlinear Physics, University of Santiago de Compostela for hospitality. VPM acknowledges support by Ministerio de Economía y Competitividad and Xunta de Galicia (MAT2015-71119-R, GPC2015/014), and contributions by the COST Action MP1305 and CRETUS Strategic Partnership (AGRUP2015/02).

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35. The mean degree and clustering coefficient remain constant up to $t \approx 0.5$ and then vary. From $t \approx 5$ no further changes are observed. In our simulations we estimate the half life of edges as $t_1 \approx 0.5 - 0.9$ for the shear flow. For $N = 900$ particles the graph typically contains a few thousand links. Using a rough argument, we estimate that the majority of links will have undergone changes after about ten half lives, i.e., $t_2 \approx 5$.