

LETTERS

Mobility promotes and jeopardizes biodiversity in rock–paper–scissors games

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Biodiversity is essential to the viability of ecological systems. Species diversity in ecosystems is promoted by cyclic, non-hierarchical interactions among competing populations. Central features of such non-transitive relations are represented by the ‘rock–paper–scissors’ game, in which rock crushes scissors, scissors cut paper, and paper wraps rock. In combination with spatial dispersal of static populations, this type of competition results in the stable coexistence of all species and the long-term maintenance of biodiversity^{1–5}. However, population mobility is a central feature of real ecosystems: animals migrate, bacteria run and tumble. Here, we observe a critical influence of mobility on species diversity. When mobility exceeds a certain value, biodiversity is jeopardized and lost. In contrast, below this critical threshold all subpopulations coexist and an entanglement of travelling spiral waves forms in the course of time. We establish that this phenomenon is robust; it does not depend on the details of cyclic competition or spatial environment. These findings have important implications for maintenance and temporal development of ecological systems and are relevant for the formation and propagation of patterns in microbial populations or excitable media.

The remarkable biodiversity present in ecosystems confounds a naive interpretation of darwinian evolution in which interacting species compete for limited resources until only the fitter species survives. As a striking example, consider that a 30 g sample of soil from a Norwegian forest is estimated to contain some 20,000 common bacterial species⁶. Evolutionary game theory^{7–9}, in which the success of one species relies on the behaviour of others, provides a useful framework in which to investigate co-development of populations theoretically. In this context, the rock–paper–scissors game has emerged as a paradigm to describe species diversity^{1–5,10–12}. If three subpopulations interact in this non-hierarchical way, we intuitively expect that diversity may be preserved: Each species dominates another only to be outperformed by the remaining one in an endlessly spinning wheel of species chasing species.

Communities of subpopulations exhibiting such dynamics have been identified in numerous ecosystems, ranging from coral reef invertebrates¹³ to lizards in the inner Coast Range of California¹⁴. In particular, recent experimental studies using microbial laboratory cultures have been devoted to the influence of spatial structure on time development and coexistence of species^{3,15}. Investigating three strains of colicinogenic *Escherichia coli* in different environments, it has been shown that cyclic dominance alone is not sufficient to preserve biodiversity. Only when the interactions between individuals are local (for example, bacteria arranged on a Petri dish) can spatially separated domains dominated by one subpopulation form and lead to stable coexistence^{1,3}.

Here we show that biodiversity is affected drastically by spatial migration of individuals, a ubiquitous feature of real ecosystems.

Migration competes with local interactions such as reproduction and selection, thereby mediating species preservation and biodiversity. For low values of mobility, the temporal development is dominated by interactions among neighbouring individuals, resulting in the long-term maintenance of species diversity. In contrast, when species mobility is high, spatial homogeneity results and biodiversity is lost. Interestingly, a critical value of mobility sharply delineates these two scenarios. We obtain concise predictions for the fate of the ecological system as a function of species mobility, thereby gaining a comprehensive understanding of its biodiversity.

The influence of mobility on species coexistence was previously studied within the framework of coupled habitat patches (“island models”)^{16–19}. In particular, Levin considered an idealized two-patch system and observed a critical mobility for stable coexistence¹⁶. Other models comprising many spatially arranged patches were shown to facilitate pattern formation^{17,18}. Because often in nature spatial degrees of freedom vary continuously (for example, bacteria can visit the entire area of a Petri dish), we relax the simplifying assumption of habitat patches and consider continuous spatial distribution of individuals. Moreover, as an inherent feature of real ecosystems and in contrast to previous deterministic investigations^{16–19}, we explicitly take the stochastic character of the interactions among the populations into account. Such interacting particle systems, where individuals are discrete and space is treated explicitly, have already been considered in ecological contexts^{1,2,4,5,20}. The behaviour of these models often differs from what is inferred from deterministic reaction–diffusion equations, or from interconnected patches²⁰. In the case of cyclic competition, such stochastic spatial systems have been shown to allow for stable coexistence of all species^{1,2,4,5} when individuals are static. Here we explore the novel features emerging from individuals’ mobility.

Consider mobile individuals of three subpopulations (referred to as A, B and C), arranged on a spatial lattice, where they can only interact with nearest neighbours. For the possible interactions, we consider a version of the rock–paper–scissors game, namely a stochastic spatial variant of the model introduced in 1975 by May and Leonard¹⁰ (see Methods). Schematic illustrations of the model’s dynamics are provided in Fig. 1. The basic reactions comprise selection and reproduction processes, which occur at rates σ and μ , respectively. Individuals’ mobility stems from the possibility that two neighbouring individuals will swap their position (at rate ε) and will move to an adjacent empty site: hence, individuals randomly migrate on the lattice. We define the length of the square lattice as the size unit, and denote by N the number of sites. Within this setting, and applying the theory of random walks²¹, the typical area explored by one mobile individual per unit time is proportional to $M = 2\varepsilon N^{-1}$, which we refer to as the mobility. The interplay of the latter with selection and reproduction processes sensitively

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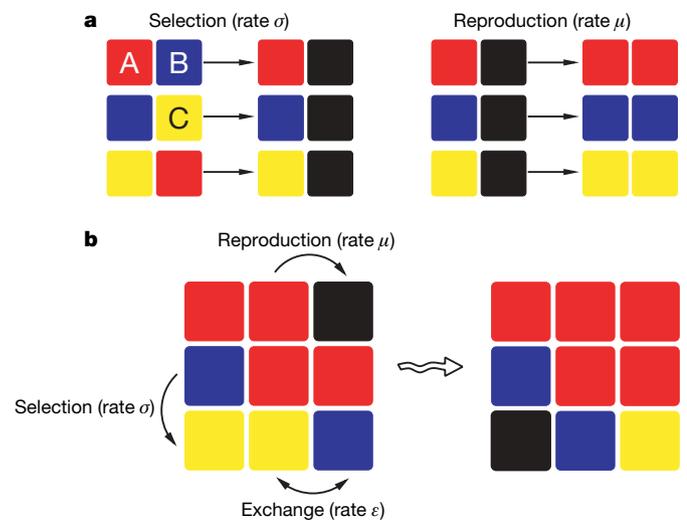


Figure 1 | The rules of the stochastic model. Individuals of three competing species A (red), B (blue), and C (yellow) occupy the sites of a lattice. **a**, They interact with their nearest neighbours through selection or reproduction, both of which reactions occur as Poisson processes at rates σ and μ , respectively. Selection reflects cyclic dominance: A can kill B, yielding an empty site (black). In the same way, B invades C, and C in turn outcompetes A. Reproduction of individuals is only allowed on empty neighbouring sites, to mimic a finite carrying capacity of the system. We also endow individuals with mobility: at exchange rate ϵ , they are able to swap position with a neighbouring individual or hop onto an empty neighbouring site (exchange). **b**, An example of the three processes, taking place on a 3×3 square lattice.

determines whether species can coexist on the lattice or not, as discussed below.

We performed extensive computer simulations of the stochastic system (see Methods) and typical snapshots of the steady states are reported in Fig. 2. When the mobility of the individuals is low, we find that all species coexist and self-arrange by forming patterns of moving spirals. With increasing mobility M , these structures grow in size, and disappear for large enough M . In the absence of spirals, the system adopts a uniform state where only one species is present, while the others have died out. Which species remains is subject to a random process, all species having equal chances to survive in our model.

We obtain concise predictions on the stability of three-species coexistence by adapting the concept of extensivity from statistical physics (see Supplementary Notes). We consider the typical waiting time T until extinction occurs, and its dependence on the system size N . If $T(N) \propto N$, the stability of coexistence is marginal¹². Conversely, longer (shorter) waiting times scaling with higher (lower) powers of N indicate stable (unstable) coexistence. These three scenarios can be distinguished by computing the probability P_{ext} that two species have gone extinct after a waiting time $t \propto N$. In Fig. 2, we report the dependence of P_{ext} on the mobility M . For illustration, we have considered equal reaction rates for selection and reproduction, and, without loss of generality, set the time-unit by fixing $\sigma = \mu = 1$. With increasing system size N , a sharpened transition emerges at a critical value $M_c = (4.5 \pm 0.5) \times 10^{-4}$ for the fraction of the entire lattice area explored by an individual in one time-unit. Below M_c , the extinction probability P_{ext} tends to zero as the system size increases, and coexistence is stable (implying super-persistent

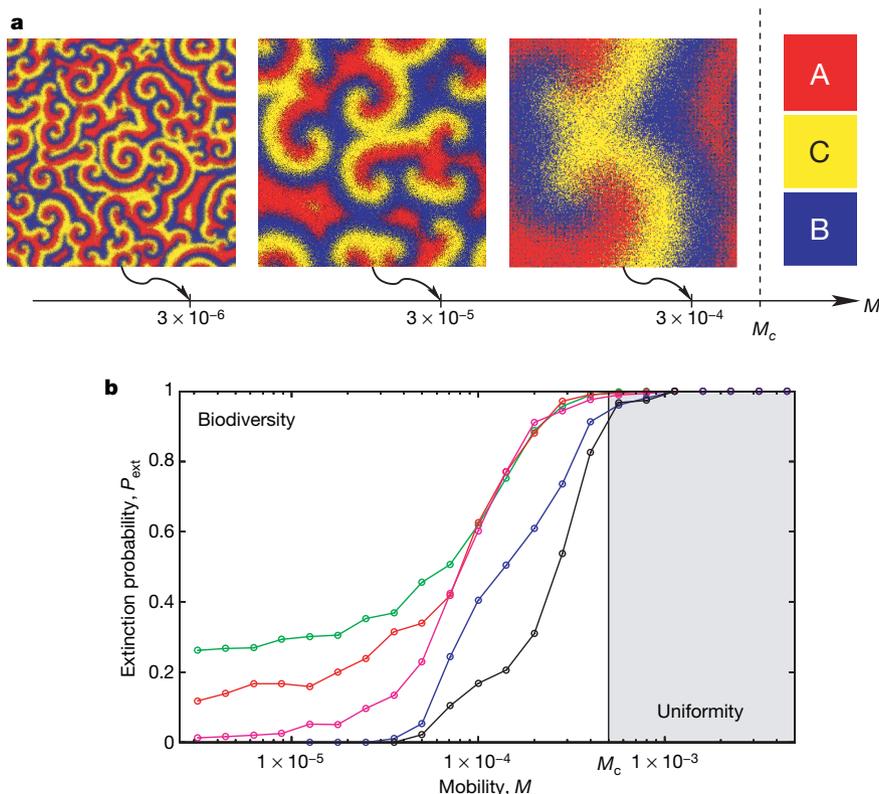


Figure 2 | The critical mobility M_c . Mobility below the value M_c induces biodiversity; while it is lost above that threshold. **a**, We show snapshots obtained from lattice simulations of typical states of the system after long temporal development (that is, at time $t \propto N$) and for different values of M (each colour represents one of the three species and black dots indicate empty spots). With increasing M (from left to right), the spiral structures grow, and outgrow the system size at the critical mobility M_c . Then coexistence of all three species is lost and uniform populations remain

(right). **b**, Quantitatively, we have considered the extinction probability P_{ext} that, starting with randomly distributed individuals on a square lattice, the system has reached an absorbing state after a waiting time $t = N$. We compute P_{ext} as a function of the mobility M (and $\sigma = \mu = 1$), and show results for different system sizes: $N = 20 \times 20$ (green), $N = 30 \times 30$ (red), $N = 40 \times 40$ (purple), $N = 100 \times 100$ (blue), and $N = 200 \times 200$ (black). As the system size increases, the transition from stable coexistence ($P_{\text{ext}} = 0$) to extinction ($P_{\text{ext}} = 1$) sharpens at a critical mobility $M_c = (4.5 \pm 0.5) \times 10^{-4}$.

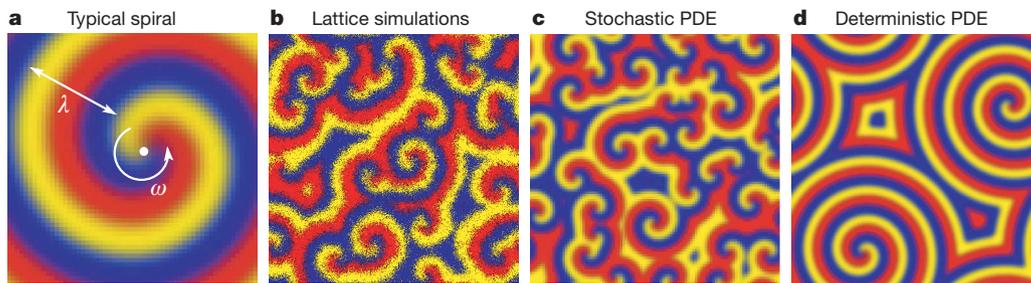


Figure 3 | Spiralling patterns. **a**, Typical spiral (schematic). It rotates around the origin (white dot) at a frequency ω and possesses a wavelength λ . **b**, In our lattice simulations, when the mobility of individuals lies below the critical value, all three species coexist, forming mosaics of entangled, rotating spirals (each colour represents one of the species and black dots indicate empty spots). **c**, We have found that the system's development can aptly be described by stochastic PDE. In the case of lattice simulations and stochastic PDE, internal noise acts as a source of local inhomogeneities and ensures the robustness of the dynamical behaviour: the spatio-temporal

patterns are independent of the initial conditions. **d**, Ignoring the effects of noise, we are left with deterministic PDE that also give rise to spiralling structures. The latter share the same wavelength and frequency with those of the stochastic description but, in the absence of fluctuations, their overall size and number depend on the initial conditions and can deviate significantly from their stochastic counterparts. In **b** and **c**, the system is initially in a homogeneous state, while **d** has been generated by considering an initial local perturbation. Parameters are $\sigma = \mu = 1$ and $M = 1 \times 10^{-5}$.

transients²²; see Supplementary Notes). On the other hand, above the critical mobility, the extinction probability approaches 1 for large system size, and coexistence is unstable. One of our central results is that we have identified a mobility threshold for biodiversity:

There exists a critical value M_c such that a low mobility $M < M_c$ guarantees coexistence of all three species, while $M > M_c$ induces extinction of two of them, leaving a uniform state with only one species.

To give a biological illustration of this statement, let us consider colicinogenic strains of *E. coli* growing on a Petri dish³. In this setting, ten bacterial generations have been observed in 24 h, yielding selection and reproduction rates of about ten per day. The typical size of a Petri dish is roughly 10 cm, so we have evaluated the critical mobility to be about $5 \times 10^2 \mu\text{m}^2 \text{s}^{-1}$. Comparing that estimate to the mobility of *E. coli*, we find that it can, by swimming and tumbling in super-soft agar, explore areas of more than $10^3 \mu\text{m}^2 \text{s}^{-1}$ (ref. 23). This value can be considerably lowered by increasing the agar concentration.

When the mobility is low ($M < M_c$), the interacting subpopulations exhibit fascinating patterns, as illustrated by the snapshots of Fig. 2. The emerging reactive states are formed by an entanglement of spiral waves, characterizing the competition among the species which endlessly hunt each other, as illustrated in Supplementary Videos 1 and 2 (see also Supplementary Discussion). Formation of this type of patterns has been observed in microbial populations, such as myxobacteria aggregation²⁴ or multicellular *Dictyostelium* mounds²⁵, as well as in cell signalling and control²⁶. Remarkably, a mathematical description and techniques borrowed from the theory of stochastic processes²⁷ allow us to obtain these complex structures by means of stochastic partial differential equations (PDE), see Fig. 3 and Methods. Furthermore, recasting the dynamics in the form of a complex Ginzburg–Landau equation^{28,29} allows us to obtain analytical expressions for the spirals' wavelength λ and frequency (see Supplementary Notes). These results, up to a constant prefactor, agree with those of numerical computations, and will be published elsewhere (manuscript in preparation).

As shown in Fig. 2, the spirals' wavelength λ rises with the individuals' mobility. Our analysis reveals that the wavelength is proportional to \sqrt{M} (see Supplementary Notes). This relation holds up to the mobility M_c , where a critical wavelength λ_c is reached. For mobilities above the threshold M_c , the spirals' wavelength λ exceeds the critical value λ_c and the patterns outgrow the system size, causing the loss of biodiversity (see Fig. 2). We have found λ_c to be universal, that is, independent on the selection and reproduction rates. This is not the case for M_c , whose value varies with these parameters (see Supplementary Notes). Using lattice simulations, stochastic PDE and the properties of the complex Ginzburg–Landau equation, we have derived the dependence of the critical mobility $M_c(\mu)$ on the

reproduction rate μ (where the time-unit is set by keeping $\sigma = 1$). This enables us to analytically predict, for all values of parameters, whether biodiversity is maintained or lost. We have summarized these results in a phase diagram, reported in Fig. 4. We identify a uniform phase, in which two species go extinct (when $M > M_c(\mu)$), and a biodiverse phase (when $M < M_c(\mu)$) with coexistence of all species and propagation of spiral waves.

The generic ingredients required for the above scenario to hold are the mobility of the individuals and a cyclic dynamics exhibiting an unstable reactive fixed point. The underlying mathematical description of this class of dynamical systems is derived in terms of complex Ginzburg–Landau equations. Their universality classes reveal the robustness of the phenomena which we have reported above, that is, the existence of a critical mobility and the emergence of spiral waves; they are not restricted to specific details of the model.

Our study has direct implications for experimental research on biodiversity and pattern formation. As an example, one can envisage

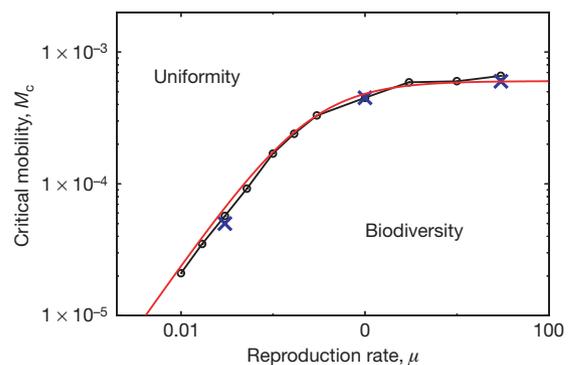


Figure 4 | Phase diagram. The critical mobility M_c as a function of the reproduction rate μ yields a phase diagram with a phase where biodiversity is maintained as well as a uniform one where two species go extinct. The time unit is set by $\sigma = 1$. On the one hand, we have computed M_c from lattice simulations, using different system sizes. The results are shown as blue crosses. On the other hand, we have calculated M_c using the approach of stochastic PDE (black dots, black lines are a guide to the eye) as well as analytically via the complex Ginzburg–Landau equation (red line). When we vary the reproduction rate, two different regimes emerge. If μ is much smaller than the selection rate, that is, $\mu \ll \sigma$, reproduction is the dominant limiter of the temporal development. In this case, there is a linear relation with the critical mobility, that is $M_c \propto \mu$, as follows from dimensional analysis. In the opposite case, if reproduction occurs much faster than selection ($\mu \gg \sigma$), the latter limits the dynamics and M_c depends linearly on σ , so that $M_c \propto \sigma$. Here, as $\sigma = 1$ is kept fixed (time-scale unit), this behaviour is reflected in the fact that M_c approaches a constant value for $\mu \gg \sigma$.

an experiment extending the study³ on colicinogenic *E. coli*. Allowing the bacteria to migrate in soft agar on a Petri dish should, for low mobilities, result in stable coexistence promoted by the formation of spiral patterns. Increasing the mobility (for example, on super-soft agar), the patterns should grow in size and finally outgrow the system at some critical value, corresponding to the threshold M_c discussed above. For even higher values of the mobility, biodiversity should be lost after a short transient time and only one species should cover the entire Petri dish. We think that the regimes of both mobilities, corresponding to the biodiverse and uniform phases, should be experimentally accessible.

We have shown how concepts from game theory combined with methods used to study pattern formation reveal the subtle influence of mobility on the temporal development of coexisting species. Many more questions and applications regarding the seminal interplay between these different fields lie ahead. As an example, it has been shown that cyclic dominance can occur in social dilemmas^{9,30}, which suggests implications of our results for the behavioural sciences.

METHODS SUMMARY

To model cyclic dominance, we use a stochastic lattice version (following work by Durrett and Levin)² of a model proposed by May and Leonard¹⁰ in 1975. As main characteristics, in the absence of spatial structure, their equations possess a deterministically unstable fixed point associated to coexistence of all three species: in the course of time, the system spirals (in the phase space) away from coexistence and moves in turn from a state with nearly only As to another one with nearly only Bs, and then to a state with nearly only Cs.

In our stochastic lattice simulations, we have arranged the three subpopulations on a two-dimensional square lattice with periodic boundary conditions. Every lattice site is occupied by an individual of species A, species B or species C, or left empty. At each simulation step, a random individual is chosen to interact with one of its four nearest neighbours: which one is also randomly determined. Whether selection, reproduction or mobility occurs, as well as the corresponding waiting time, is computed according to the reaction rates using an efficient algorithm due to Gillespie³¹. We set one generation (when every individual has reacted on average once) as the unit of time. To compute the extinction probability, we have used different system sizes, from 20×20 to 200×200 lattice sites, and sampled between 500 and 2,000 realizations. The snapshots shown in Fig. 2 result from system sizes of up to $1,000 \times 1,000$ sites.

Our stochastic PDE consist of a mobility term, nonlinear terms describing the deterministic temporal development of the nonspatial model (May–Leonard equations), and (multiplicative) white noise; see Supplementary Notes.

We have solved the resulting equations with the help of open software from the XMDS project (<http://www.xmds.org>), using the semi-implicit method in the interaction picture (SIIP) as an algorithm, spatial meshes of 200×200 to 500×500 points, and 10,000 points in the time direction.

Received 3 May; accepted 18 July 2007.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements We thank M. Bathe and M. Leisner for discussions on the manuscript. Financial support of the German Excellence Initiative via the program “Nanosystems Initiative Munich (NIM)” as well as the SFB “Manipulation of Matter at the Nanometer Length Scale” is gratefully acknowledged. M.M. is grateful to the Alexander von Humboldt Foundation for support through a fellowship.

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