The outbreak of cooperation among success-driven individuals under noisy conditions

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According to Thomas Hobbes' *Leviathan* [1651; 2008 (Touchstone, New York), English Ed], "the life of man [is] solitary, poor, nasty, brutish, and short," and it would need powerful social institutions to establish social order. In reality, however, social cooperation can also arise spontaneously, based on local interactions rather than centralized control. The self-organization of cooperative behavior is particularly puzzling for social dilemmas related to sharing natural resources or creating common goods. Such situations are often described by the prisoner's dilemma. Here, we report the sudden outbreak of predominant cooperation in a noisy world dominated by selfishness and defection, when individuals imitate superior strategies and show success-driven migration. In our model, individuals are unrelated, and do not inherit behavioral traits. They defect or cooperate selfishly when the opportunity arises, and they do not know how often they will interact or have interacted with someone else. Moreover, our individuals have no reputation mechanism to form friendship networks, nor do they have the option of voluntary interaction or costly punishment. Therefore, the outbreak of prevailing cooperation, when directed motion is integrated in a game-theoretical model, is remarkable, particularly when random strategy mutations and random relocations challenge the formation and survival of cooperative clusters. Our results suggest that mobility is significant for the evolution of social order, and essential for its stabilization and maintenance.

evolution | pattern formation | spatial games | mobility | migration

Although the availability of new data of human mobility has revealed relations with social communication patterns (1) and epidemic spreading (2), its significance for the cooperation among individuals is still widely unknown. This is surprising, because migration is a driving force of population dynamics as well as urban and interregional dynamics (3–5).

Below, we model cooperation in a game-theoretical way (6–8), and integrate a model of stylized relocations. This is motivated by the observation that individuals prefer better neighborhoods, e.g., a nicer urban quarter or a better work environment. To improve their situation, individuals are often willing to migrate. In our model of success-driven migration, individuals consider different alternative locations within a certain migration range, reflecting the effort they are willing or able to spend on identifying better neighborhoods. How favorable a new neighborhood is expected to be is determined by test interactions with individuals in that area ("neighborhood testing"). The related investments are often small compared with the potential gains or losses after relocating, i.e., exploring new neighborhoods is treated as "fictitious play." Finally, individuals are assumed to move to the tested neighborhood that promises to be the best.

So far, the role of migration has received relatively little attention in game theory (9–16), probably because it has been found that mobility can undermine cooperation by supporting defector invasion (11, 12). However, this primarily applies to cases, where individuals choose their new location in a random (e.g., diffusive) way. In contrast, extending spatial games by the specific mechanism of *success-driven* migration can support the survival and spreading of cooperation. As we will show, it even promotes the spontaneous *outbreak* of prevalent cooperation in a world of selfish individuals with various sources of randomness ("noise"), starting with defectors only.

Model

Our study is carried out for the prisoner's dilemma game (PD). This has often been used to model selfish behavior of individuals in situations where it is risky to cooperate and tempting to defect, but where the outcome of mutual defection is inferior to cooperation on both sides (7, 17). Formally, the so-called "reward" R represents the payoff for mutual cooperation, whereas the payoff for defection on both sides is the "punishment" P. T represents the "temptation" to unilaterally defect, which results in the "sucker's payoff" S for the cooperating individual. Given the inequalities $T > R > P > S$ and $2R > T + S$, which define the classical prisoner's dilemma, it is more profitable to defect, no matter what strategy the other individual selects. Therefore, rationally behaving individuals would be expected to defect when they meet *once*. However, defection by everyone is implied as well by the game-dynamical replicator equation (10), which takes into account imitation of superior strategies, or payoff-driven birth-and-death processes. In contrast, a coexistence of cooperators and defectors is predicted for the snowdrift game (SD). Although it is also used to study social cooperation, its payoffs are characterized by $T > R > S > P$ (i.e., $S > P$ rather than $P > S$).

As is well-known (17), cooperation can, for example, be supported by repeated interactions (7), by intergroup competition with or without altruistic punishment (18–20), and by network reciprocity based on the clustering of cooperators (21–23). In the latter case, the level of cooperation in 2-dimensional spatial games is further enhanced by "disordered environments" ($\approx$10% inaccessible empty locations) (24), and by diffusive mobility, provided that the mobility parameter is in a suitable range (16). However, strategy mutations, random relocations, and other sources of stochasticity ("noise") can significantly challenge the formation and survival of cooperative clusters. When no mobility or undirected, random mobility are considered, the level of cooperation in the spatial games studied by us is sensitive to noise (see Figs. 1*D* and 3*C*), as favorable correlations between cooperative neighbors are destroyed. *Success-driven* migration, in contrast, is a robust mechanism. By leaving unfavorable neighborhoods, seeking more favorable ones, and remaining in cooperative neighborhoods, it supports cooperative clusters very efficiently against the destructive effects of noise, thus preventing defector invasion in a large area of payoff parameters. We assume N individuals on a square

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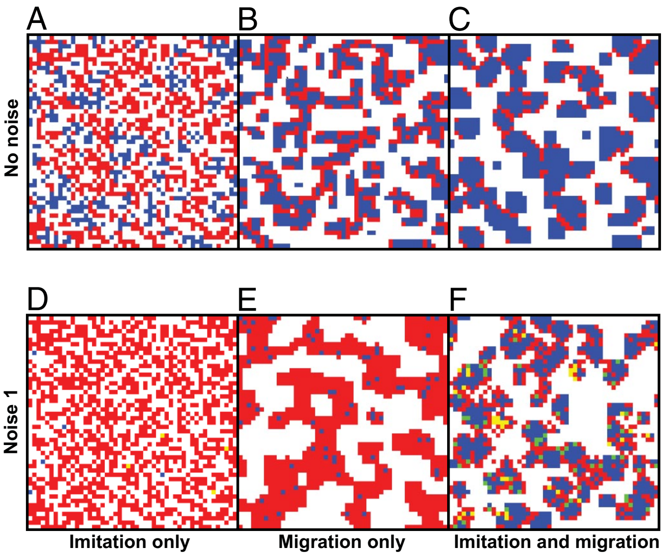

Fig. 1. Representative simulation results for the spatial prisoner's dilemma with payoffs $T = 1.3$, $R = 1$, $P = 0.1$, and $S = 0$ after $t = 200$ iterations. The simulations are for 49×49 grids with 50% empty sites. At time $t = 0$ we assumed that 50% of the individuals were cooperators and 50% were defectors. Both strategies were homogeneously distributed over the whole grid. For reasons of comparison, all simulations were performed with identical initial conditions and random numbers (red, defector; blue, cooperator; white, empty site; green, defector who became a cooperator in the last iteration; yellow, cooperator who turned into a defector). Compared with simulations without noise (*Upper*), the strategy mutations of noise 1 with $r = q = 0.05$ not only reduce the resulting level of cooperation, but also the outcome and pattern formation dynamics, even if the payoff values, initial conditions, and update rules are the same (*Lower*). In the imitation-only case with $M = 0$ that is displayed on the left, the initial fraction of 50% cooperators is quickly reduced because of imitation of more successful defectors. The result is a "frozen" configuration without any further strategy changes. (*A*) In the noiseless case, a certain number of cooperators can survive in small cooperative clusters. (*D*) When noise 1 is present, random strategy mutations destroy the level of cooperation almost completely, and the resulting level of defection reaches values close to 100%. The illustrations in the center show the migration-only case with mobility range $M = 5$. (*B*) When no noise is considered, small cooperative clusters are formed, and defectors are primarily located at their boundaries. (*E*) In the presence of noise 1, large clusters of defectors are formed instead, given $P > 0$. The illustrations on the right show the case where imitation is combined with success-driven migration (here, $M = 5$). (*C*) In the noiseless case, cooperative clusters grow and eventually freeze (i.e., strategy changes or relocations do not occur any longer). (*F*) Under noisy conditions, in contrast, the cooperative clusters continue to adapt and reconfigure themselves, as the existence of yellow and green sites indicates.

lattice with periodic boundary conditions and $L \times L$ sites, which are either empty or occupied by one individual. Individuals are updated asynchronously, in a random sequential order. The randomly selected individual performs simultaneous interactions with the $m = 4$ direct neighbors and compares the overall payoff with that of the m neighbors. Afterward, the strategy of the best performing neighbor is copied with probability $1 - r$ ("imitation"), if the own payoff was lower. With probability r, however, the strategy is randomly "reset": **Noise 1** assumes that an individual spontaneously chooses to cooperate with probability q or to defect with probability $1 - q$ until the next strategy change. The resulting strategy mutations may be considered to reflect deficient imitation attempts or trial-and-error behavior. As a side effect, such noise leads to an independence of the finally resulting level of cooperation from the initial one at $t = 0$, and a *qualitatively different* pattern formation dynamics for the same payoff values, update rules, and initial conditions (see supporting information (SI) Fig. S1). Using the alternative Fermi update rule (22) would have been possible as well. However, resetting strategies rather than inverting them, combined with values q much smaller than 1/2, has here the advantage of creating particularly adverse conditions for cooperation, independently of what strategy prevails. Below, we want to learn whether predominant cooperation can survive or even emerge under such adverse conditions. "Success-driven migration" has been implemented as follows (9, 25). Before the imitation step, an individual explores the expected payoffs for the empty sites in the migration neighborhood of size $(2M + 1) \times (2M + 1)$ (the Moore neighborhood of range M). If the fictitious payoff is higher than in the current location, the individual is assumed to move to the site with the highest payoff and, in the case of several sites with the same payoff, to the closest one (or one of them); otherwise it stays put.

Results

Computer simulations of the above model show that, in the *imitation-only* case of classical spatial games with noise 1, but *without* a migration step, the resulting fraction of cooperators in the PD tends to be very low. It basically reflects the fraction rq of cooperators due to strategy mutations. For $r = q = 0.05$, we find almost frozen configurations, in which only a small number of cooperators survive (see Fig. 1*D*). In the *migration-only* case without an imitation step, the fraction of cooperators changes only by strategy mutations. Even when the initial strategy distribution is uniform, one observes the formation of spatio-temporal patterns, but the patterns get almost frozen after some time (see Fig. 1*E*).

It is interesting that, although for the connectivity structure of our PD model neither imitation only (Fig. 1*D*) nor migration only (Fig. 1*E*) can promote cooperation under noisy conditions, their *combination* does. Computer simulations show the formation of cooperative clusters with a few defectors at their boundaries (see Fig. 1*F*). Once cooperators are organized in clusters, they tend to have more neighbors and to reach higher payoffs on average, which allows them to survive (9, 10, 25). It will now have to be revealed, how success-driven migration causes the *formation* of clusters at all, considering the opposing noise effects. In particular, we will study why defectors fail to invade cooperative clusters and to erode them from within, although a cooperative environment is most attractive to them.

To address these questions, Fig. 2 studies a "defector's paradise" with a single defector in the center of a cooperative cluster. In the noisy *imitation-only* spatial prisoner's dilemma, defection tends to spread up to the boundaries of the cluster, as cooperators imitate more successful defectors (see Fig. 2 *A–D*). However, if imitation is combined with *success-driven migration*, the results are in sharp contrast. Although defectors still spread initially, cooperative neighbors who are M steps away from the boundary of the cluster can now evade them. Because of this defector-triggered migration, the neighborhood reconfigures itself adaptively. For example, a large cooperative cluster may split up into several smaller ones (see Figs. 2 *E–H*). Eventually, the defectors end up at the boundaries of these cooperative clusters, where they often turn into cooperators by imitation of more successful cooperators in the cluster, who tend to have more neighbors. This promotes the spreading of cooperation (9, 10, 25).

Because evasion takes time, cooperative clusters could still be destroyed when continuously challenged by defectors, as it happens under noisy conditions. Therefore, let us now study the effect of different kinds of randomness (10, 26). **Noise 1** (defined above) assumes *strategy mutations*, but leaves the spatial distribution of individuals unchanged (see Fig. 3*A*). **Noise 2**, in contrast, assumes that individuals, who are selected with probability r, move to a randomly chosen free site without considering the expected success (*random relocations*). Such random moves

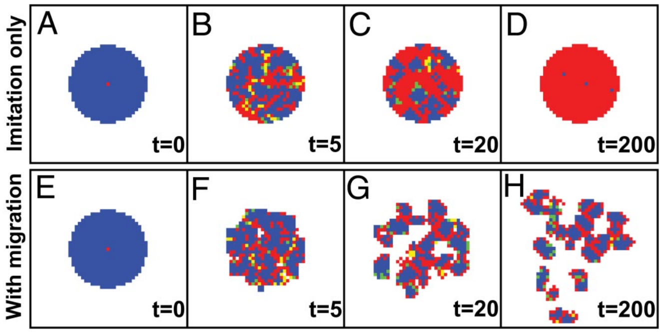

Fig. 2. Representative simulation results after $t = 200$ iterations in the "defector's paradise" scenario, starting with a single defector in the center of a cooperative cluster at $t = 0$. The simulations are performed on 49×49 grids with $n = 481$ individuals, corresponding to a circle of diameter 25. They are based on the spatial prisoner's dilemma with payoffs $T = 1.3$, $R = 1$, $P = 0.1$, and $S = 0$ and noise parameters $r = q = 0.05$ (red, defector; blue, cooperator; white, empty site; green, defector who became a cooperator; yellow, cooperator who turned into a defector in the last iteration). For reasons of comparison, all simulations were carried out with identical initial conditions and random numbers. (*A–D*) In the noisy imitation-only case with $M = 0$, defection (red) eventually spreads all over the cluster. The few remaining cooperators (blue) are due to strategy mutations. (*E–H*) When we add success-driven motion, the result is very different. Migration allows cooperators to evade defectors. That triggers a splitting of the cluster, and defectors end up on the boundaries of the resulting smaller clusters, where most of them can be turned into cooperators. This mechanism is crucial for the unexpected survival and spreading of cooperation.

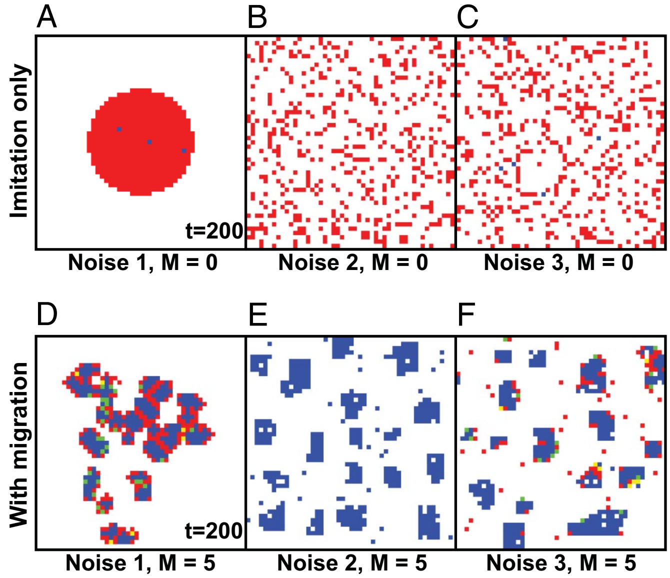

Fig. 3. Representative simulation results for the invasion scenario with a defector in the center of a cooperative cluster ("defector's paradise"). The chosen payoffs $T = 1.3$, $R = 1$, $P = 0.1$, and $S = 0$ correspond to a prisoner's dilemma. The simulations are for 49×49 grids with $n = 481$ individuals, corresponding to a circle of diameter 25 (red, defector; blue, cooperator; white, empty site; green, defector who became a cooperator; yellow, cooperator who turned into a defector in the last iteration). (*Upper*) Typical numerical results for the imitation-only case ($M = 0$) after $t = 200$ iterations: (*A*) for noise 1 (strategy mutations) with mutation rate $r = 0.05$ and creation of cooperators with probability $q = 0.05$; (*B*) for noise 2 (random relocations) with relocation rate $r = 0.05$; and (*C*) for noise 3 (a combination of random relocations and strategy mutations) with $r = q = 0.05$. Because cooperators imitate defectors with a higher overall payoff, defection spreads easily. The different kinds of noise influence the dynamics and resulting patterns considerably. Although strategy mutations in *A* and *C* strongly reduce the level of cooperation, random relocations in *B* and *C* break up spatial clusters, leading to a dispersion of individuals in space. Their combination in *C* essentially destroys both, clusters and cooperation. (*Lower*) Same for the case of imitation *and* success-driven migration with mobility range $M = 5$: (*D*) for noise 1 with $r = q = 0.05$; (*E*) for noise 2 with $r = 0.05$, and (*F*) for noise 3 with $r = q = 0.05$. Note that noise 1 just mutates strategies and does not support a spatial spreading, whereas noise 2 causes random relocations, but does not mutate strategies. This explains why the clusters in Fig. 3*D* do not spread out over the whole space and why no new defectors are created in Fig. 3*E*. However, the creation of small cooperative clusters is found in all 3 scenarios. Therefore, it is robust with respect to various kinds of noise, in contrast to the imitation-only case.

may potentially be of long distance and preserve the number of cooperators, but have the potential of destroying spatial patterns (see Fig. 3*B*). **Noise 3** combines noise 1 and noise 2, assuming that individuals randomly relocate with probability r and additionally reset their strategy as in noise 1 (see Fig. 3*C*).

Whereas cooperation in the imitation-only case is quite sensitive to noise (see Fig. 3 *A–C*), the combination of imitation with success-driven motion is not (see Fig. 3 *D–F*). Whenever an empty site inside a cluster of cooperators occurs, it is more likely that the free site is entered by a cooperator than by a defector, as long as cooperators prevail within the migration range M. In fact, the formation of small cooperative clusters was observed for *all* kinds of noise. That is, the combination of imitation with success-driven migration is a robust mechanism to maintain and even spread cooperation under various conditions, given there are enough cooperators in the beginning.

It is interesting, whether this mechanism is also able to facilitate a spontaneous *outbreak* of predominant cooperation in a noisy world dominated by selfishness, without a "shadow of the future" (7, 27). Our simulation scenario assumes defectors only in the beginning (see Fig. 4*A*), strategy mutations in favor of defection, and short-term payoff-maximizing behavior in the vast majority of cases. To study conditions under which a significant fraction of cooperators is unlikely, our simulations are performed with noise 3 and $r = q = 0.05$, as it tends to destroy spatial clusters and cooperation (see Fig. 3*C*). By relocating 5% randomly chosen individuals in each time step, noise 3 dissolves clusters into more or less separate individuals in the imitation-only case (see Figs. 3 *B* and *C*). In the case with success-driven migration, random relocations break up large clusters into many smaller ones, which are distributed all over the space (see Figs. 3 *E* and *F* and 4*B*). Therefore, even the clustering tendency by success-driven migration can only partially compensate for the dispersal tendency by random relocations. Furthermore, the strategy mutations involved in noise 3 tend to destroy cooperation (see Fig. 3 *A* and *C*, where the strategies of 5% randomly chosen individuals were replaced by defection in 95% of the cases and by cooperation otherwise, to create conditions favoring defection, i.e., the dominant strategy in the prisoner's dilemma). Overall, as a result of strategy mutations (i.e., without the consideration of imitation processes), only a fraction $rq = 0.0025$ of all defectors turn into cooperators in each time step, whereas a fraction $r(1 - q) \approx 0.05$ of all cooperators turn into defectors (i.e., 5% in each time step). This setting is extremely unfavorable for the spreading of cooperators. In fact, defection prevails for an extremely long time (see Figs. 4*B* and 5*A*). However, suddenly, when a small, supercritical cluster of cooperators has occurred by coincidence (see Fig. 4*C*), the fraction of cooperators spreads quickly (see Fig. 5*A*), and soon cooperators prevail (see Figs. 4*D* and 5*B*). Note that this spontaneous birth of predominant cooperation in a world of defectors does not occur in the noisy imitation-only case and demonstrates that success-driven migration can overcome the dispersive tendency of noises 2 and 3, if r is moderate and q has a finite value. That is, success-driven migration generates spatial correlations between cooperators more quickly than these noises can destroy

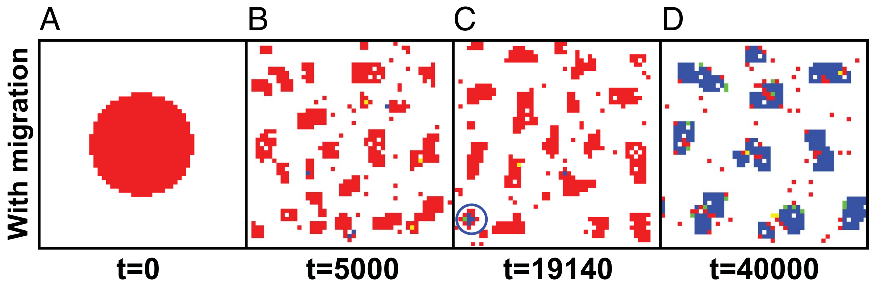

Fig. 4. Spontaneous outbreak of prevalent cooperation in the spatial prisoner's dilemma with payoffs $T = 1.3$, $R = 1$, $P = 0.1$, $S = 0$ in the presence of noise 3 (random relocations and strategy mutations) with $r = q = 0.05$. The simulations are for 49×49 grids (red, defector; blue, cooperator; white, empty site; green, defector who became a cooperator; yellow, cooperator who turned into a defector in the last iteration). (*A*) Initial cluster of defectors, which corresponds to the *final* stage of the *imitation-only* case with strategy mutations according to noise 1 (see Fig. 2*D*). (*B*) Dispersal of defectors by noise 3, which involves random relocations. A few cooperators are created randomly by strategy mutations with the very small probability $rq = 0.0025$ (0.25%). (*C*) Occurrence of a supercritical cluster of cooperators after a very long time (see blue circle). This cooperative "nucleus" originates by random coincidence of favorable strategy mutations in neighboring sites. (*D*) Spreading of cooperative clusters in the whole system. This spreading, despite the destructive effects of noise, requires an effective mechanism to form growing cooperative clusters (such as success-driven migration) and cannot be explained by random coincidence. See the Movie S1 for an animation of the outbreak of cooperation for a different initial condition.

them. This changes the outcome of spatial games essentially, as a comparison of Fig. 2 *A–D* with Fig. 4 *A–D* shows.

The conditions for the spreading of cooperators from a supercritical cluster ("nucleus") can be understood by configurational analysis (26, 28) (see Fig. S1), but the underlying argument can be both, simplified and extended. According to Fig. 6*A*, the level of cooperation changes when certain lines (or, more generally, certain hyperplanes) in the payoff-parameter space are crossed. These hyperplanes are all of the linear form

$$n_1R + n_2S = n_3T + n_4P, \qquad [1]$$

where $n_k \in \{0,1,2,3,4\}$. The left-hand side of Eq. **1** represents the payoff of the most successful cooperative neighbor of a focal individual, assuming that this has n_1 cooperating and n_2 defecting neighbors, which implies $n_1 + n_2 \leq m = 4$. The right-hand side reflects the payoff of the most successful defecting neighbor, assuming that n_3 is the number of his/her cooperating neighbors and n_4 the number of defecting neighbors, which implies $n_3 + n_4 \leq m = 4$. Under these conditions, the best-performing cooperative neighbor earns a payoff of $n_1R + n_2S$, and the best-performing defecting neighbor earns a payoff of $n_3T + n_4P$. Therefore, the focal individual will imitate the cooperator, if $n_1R + n_2S > n_3T + n_4P$, but copy the strategy of the defector if $n_1R + n_2S < n_3T + n_4P$. Eq. **1** is the line separating the area where cooperators spread (above the line) from the area of defector invasion (below it) for a certain spatial configuration of cooperators and defectors (see Fig. 6*A*). Every spatial configuration is characterized by a set of n_k parameters. As expected, the relative occurrence frequency of each configuration depends on the migration range M (see Fig. 6*B*). Higher values of M naturally create better conditions for the spreading of cooperation, because there is a larger choice of potentially more favorable neighborhoods.

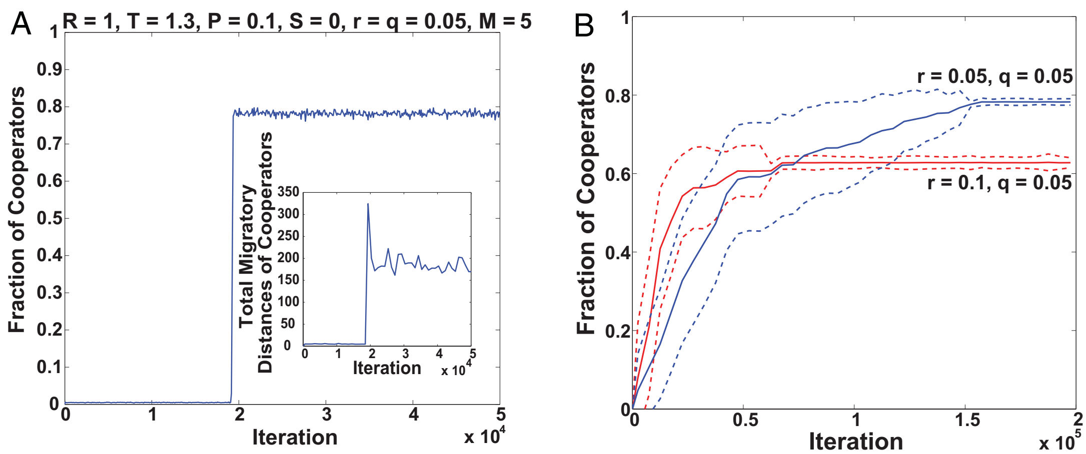

Fig. 5. Representative example for the outbreak of predominant cooperation in the prisoner's dilemma with payoffs $T = 1.3$, $R = 1$, $P = 0.1$, $S = 0$, in the presence of noise 3 with $r = q = 0.05$. The simulations are for 49×49 grids with a circular cluster of defectors and no cooperators in the beginning (see Fig. 4*A*). (*A*) After defection prevails for a very long time (here, for almost 20,000 iterations), a sudden transition to a large majority of cooperators is observed. (*Inset*) The overall distance moved by all individuals during one iteration has a peak at the time when the outbreak of cooperation is observed. Before, the rate of success-driven migration is very low, while it stabilizes at an intermediate level afterward. This reflects a continuous evasion of cooperators from defectors and, at the same time, the continuous effort to form and maintain cooperative clusters. The graph displays the amount of success-driven migration only, whereas the effect of random relocations is not shown. (*B*) Evaluating 50 simulation runs, the error bars (representing 3 standard deviations) show a large variation of the time points when prevalent cooperation breaks out. Because this time point depends on the coincidence of random cooperation in neighboring sites, the large error bars have their natural reason in the stochasticity of this process. After a potentially very long time period, however, all systems end up with a high level of cooperation. The level of cooperation decreases with the noise strength r, as expected, but moderate values of r can even *accelerate* the transition to predominant cooperation. By using the parameter values $r = 0.1$ and $q = 0.2$, the outbreak of prevalent cooperation often takes <200 iterations.

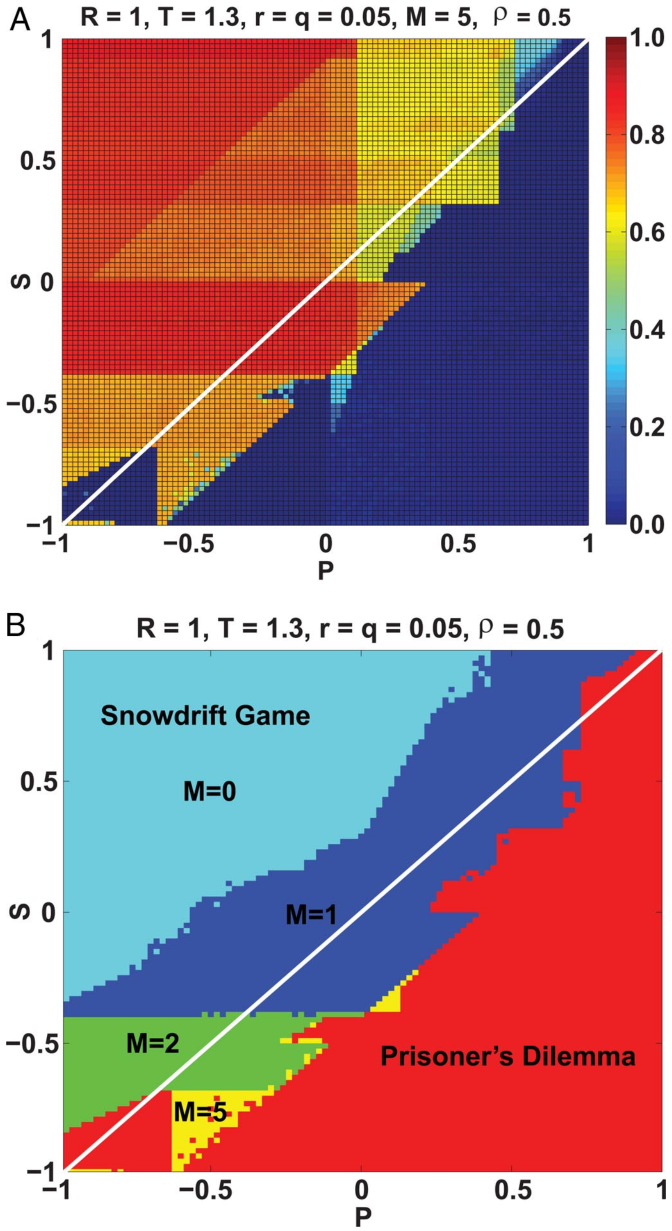

Fig. 6. Dependence of the fraction of cooperators for given payoff parameters $T = 1.3$ and $R = 1$ on the parameters P and S. The area above the solid diagonal line corresponds to the snowdrift game, the area below to the prisoner's dilemma. Our simulations were performed for grids with $L \times L = 99 \times 99$ sites and $n = L^2/2$ individuals, corresponding to a density $\rho = N/L^2 = 0.5$. At time $t = 0$ we assumed 50% of the individuals to be cooperators and 50% defectors. Both strategies were homogeneously distributed over the whole grid. The finally resulting fraction of cooperators was averaged at time $t = 200$ over 50 simulation runs with different random realizations. The simulations were performed with noise 3 (random relocations with strategy mutations) and $r = P = 0.05$. An enhancement in the level of cooperation (often by >100%) is observed mainly in the area with $P - 0.4 < S < P + 0.4$ and $P < 0.7$. Results for the noiseless case with $r = 0$ are shown in Fig. S2*a*. The fraction of cooperators is represented by color codes (see the bar to the right of the figure, where dark orange, for example, corresponds to 80% cooperators). It can be seen that the fraction of cooperators is approximately constant in areas limited by straight lines (mostly triangular and rectangular ones). These lines correspond to Eq. **1** for different specifications of n_1, n_2, n_3, and n_4 (see main text for details). (*B*) The light-blue area reflects the parameters for which cooperators reach a majority in the imitation-only case with $M = 0$. For all payoffs P and S corresponding to a prisoner's dilemma, cooperators are clearly in the minority, as expected. However, taking into account success-driven migration changes the situation in a pronounced way: For a mobility range $M = 1$, the additional area with >50% cooperators is represented by dark blue, the further extended area of prevailing cooperation for $M = 2$ by green, and for $M = 5$ by yellow. If $M = 5$, defectors are in the majority only for parameter combinations falling into the red area. This demonstrates that success-driven migration can promote predominant cooperation in considerable areas, where defection would prevail without migration. For larger interaction neighborhoods m, e.g., $m = 8$, the area of prevalent cooperation is further increased overall (data not shown). Note that the irregular shape of the separating lines is no artifact of the computer simulation or initial conditions. It results by superposition of the areas defined by Eq. **1** (see *A*).

Fig. 6*B* also shows that success-driven migration extends the parameter range, in which cooperators prevail, from the parameter range of the snowdrift game with $S > P$ to a considerable parameter range of the prisoner's dilemma. For this to happen, it is important that the attraction of cooperators is mutual, and the attraction of defectors to cooperators is not. More specifically, the attraction of cooperators is proportional to $2R$, but the attraction between defectors and cooperators is proportional to $T + S$. The attraction between cooperators is stronger, because the prisoner's dilemma usually assumes the inequality $2R > T + S$.

Besides the speed of finding neighbors to interact with, the timescales of configurational changes and correlations matter as well. By entering a cooperative cluster, a defector triggers an avalanche of strategy changes and relocations, which quickly destroys the cooperative neighborhood. During this process, individuals may alter their strategy many times, because they realize opportunities by cooperation or defection immediately. In contrast, if a cooperator joins a cooperative cluster, this will stabilize the cooperative neighborhood. Although cooperative clusters continuously adjust their size and shape, the average time period of their existence is longer than the average time period after which individuals change their strategy or location. This coevolution of social interactions and strategic behavior reflects features of many social environments. Although the latter come about by individual actions, a suitable social context can make the average behavior of individuals more predictable, which establishes a reinforcement process. For example, because of the clustering tendency of cooperators, the likelihood of finding another cooperator in the neighborhood of a cooperator is >1/2, the likelihood that a cooperator will cooperate in the next iteration.

Discussion

It is noteworthy that all of the above features—the survival of cooperation in a large-parameter area of the PD, spatiotemporal pattern formation, noise resistance, and the outbreak of predominant cooperation—can be captured by considering a mechanism as simple as success-driven migration. Success-driven migration *destabilizes* a homogeneous strategy distribution (compare Fig. 1 *C* with *A* and Fig. 1 *F* with *D*). This triggers the spontaneous formation of agglomeration and segregation patterns (29), where noise or diffusion would cause dispersal in the imitation-only case. The self-organized patterns create self-reinforcing social environments characterized by behavioral correlations, and imitation promotes the further growth of supercritical cooperation clusters. Although each mechanism by itself tends to produce frozen spatial structures, the combination of imitation and migration supports adaptive patterns (see Fig. 1*F*). This facilitates, for example, the regrouping of a cluster of cooperators on invasion by a defector, which is crucial for the survival and success of cooperators (see Fig. 2 *E*–*H*).

By further simulations we have checked that our conclusions are robust with respect to using different update rules, adding birth and death processes, or introducing a small fraction of individuals defecting unconditionally. The same applies to various kinds of "noise." Noise can even trigger cooperation in a world full of defectors, when the probability of defectors to turn spontaneously into cooperators is 20 times smaller than the probability of cooperators to turn into defectors. Compared with the implications of the game-dynamical replicator equation, this is remarkable. Although the replicator equation predicts that the stationary solution with a majority of cooperators is *un*stable with respect to perturbations and the stationary solution with a majority of defectors is stable (10), success-driven migration *inverts* the situation: The state of 100% defectors becomes *unstable* to noise, whereas a majority of cooperators is stabilized in a considerable area of the payoff parameter space.

Our results help to explain why cooperation can be frequent even if individuals would behave selfishly in the vast majority of interactions. Although one may think that migration would weaken social ties and cooperation, there is another side of it that helps to establish cooperation in the first place, without the need to modify the payoff structure. We suggest that, besides the ability for strategic interactions and learning, the ability to *move* has played a crucial role for the evolution of large-scale cooperation and social behavior. Success-driven migration can reduce unbalanced social interactions, where cooperation is unilateral, and support local agglomeration. In fact, it has been pointed out that local agglomeration is an important precondition for the evolution of more sophisticated kinds of cooperation (30). For example, the level of cooperation could be further improved by combining imitation and success-driven migration with other mechanisms such as costly punishment (19, 20), volunteering (22), or reputation (31–33).

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