

# Supplementary information

## Pair approximation

In the case of pure strategies, an analytical approximation of the spatial dynamics can be obtained through pair approximation. Instead of considering the frequency of strategies as in well-mixed populations, i.e. in mean-field theory, pair approximation tracks the frequencies of strategy pairs. Such pair configurations  $p_{s,s'}$  indicate the probability of finding an individual playing strategy  $s$  accompanied by a neighbour playing  $s'$ . For our purposes  $s, s'$  are either cooperation  $c$  or defection  $d$ , but the following considerations can be extended to an arbitrary finite set of strategies. Consistency with mean-field theory requires that  $p_s = \sum_{s'} p_{s,s'}$ , where the sum runs over the set of all strategies under consideration. It follows that pair configuration probabilities are symmetrical:  $p_{s,s'} = p_{s',s}$ . Configuration probabilities of larger clusters are approximated by pair configuration probabilities. For example, the probability of the three-cluster  $s, s', s''$  is given by  $p_{s,s',s''} = p_{s,s'} \cdot p_{s',s''} / p_{s'}$  where the denominator corrects for the fact that both,  $p_{s,s'}$  and  $p_{s',s''}$  include the probability for  $s'$ .

Let us consider individuals arranged on a square lattice with  $N = 4$  neighbours (Fig. 1a). A randomly chosen site with strategy  $A$  gets updated by comparing its performance to a randomly chosen neighbour with strategy  $B$ . The payoffs  $P_A, P_B$  of  $A$  and  $B$  are determined by interactions with their neighbours  $x, y, z, B$  and  $u, v, w, A$ , respectively. To complete the pair approximation, we need to derive the changes of the pair configuration probabilities, i.e. the probability that the pair  $p_{A,B}$  becomes  $p_{B,B}$ :

$$p_{A,B \rightarrow B,B} = \sum_{x,y,z} \sum_{u,v,w} f(P_B - P_A) \times \frac{p_{x,A} p_{y,A} p_{z,A} p_{A,B} p_{u,B} p_{v,B} p_{w,B}}{p_A^3 p_B^3},$$

where the transition probability  $f(P_B - P_A)$  is multiplied by the configuration probability and summed over all possible configurations (see methods for details on the transition probability  $f(P_B - P_A)$ ). Whenever  $B$  succeeds in populating site  $A$ , the pair configuration probabilities change: the probabilities  $p_{B,B}, p_{B,x}, p_{B,y}$  and  $p_{B,z}$  increase, while the probabilities  $p_{A,B}, p_{A,x}, p_{A,y}$  and  $p_{A,z}$  decrease. This leads to a set of ordinary differential equations which determine the time evolution of the system:

$$\begin{aligned} \dot{p}_{c,c} = & \sum_{x,y,z} (n_c(x,y,z) + 1) p_{d,x} p_{d,y} p_{d,z} \times \\ & \sum_{u,v,w} p_{c,u} p_{c,v} p_{c,w} f(P_c(u,v,w) - P_d(x,y,z)) - \\ & \sum_{x,y,z} n_c(x,y,z) p_{c,x} p_{c,y} p_{c,z} \times \\ & \sum_{u,v,w} p_{d,u} p_{d,v} p_{d,w} f(P_d(u,v,w) - P_c(x,y,z)) \end{aligned} \quad (1)$$

$$\begin{aligned} \dot{p}_{c,d} = & \sum_{x,y,z} (1 - n_c(x,y,z)) p_{d,x} p_{d,y} p_{d,z} \times \\ & \sum_{u,v,w} p_{c,u} p_{c,v} p_{c,w} f(P_c(u,v,w) - P_d(x,y,z)) - \\ & \sum_{x,y,z} (2 - n_c(x,y,z)) p_{c,x} p_{c,y} p_{c,z} \times \\ & \sum_{u,v,w} p_{d,u} p_{d,v} p_{d,w} f(P_d(u,v,w) - P_c(x,y,z)), \end{aligned} \quad (2)$$

where  $n_c(x,y,z)$  denotes a function which returns the number of cooperators among  $x, y, z$  and  $P_c(x,y,z), P_d(x,y,z)$  specify the payoffs of a cooperator (defector) interacting with  $x, y, z$  plus a defector (cooperator). Note that these two differential equations are sufficient because of the symmetry condition  $p_{c,d} = p_{d,c}$  and the obvious constraint  $p_{c,c} + p_{c,d} + p_{d,c} + p_{d,d} = 1$ . For simplicity, the above equations omit the common factor  $2p_{c,d} / (p_c^3 \cdot p_d^3)$ , which corresponds to a non-linear transformation of the time scale but leaves the equilibrium unaffected. The equilibrium values  $\hat{p}_{s,s'}$  are obtained either through numerical integration or by setting  $\dot{p}_{c,c} = \dot{p}_{c,d} = 0$  and solving for  $p_{c,c}, p_{c,d}$ . These equilibrium values in turn yield an approximation of the equilibrium frequencies  $\hat{p}_s = \sum_{s'} \hat{p}_{s,s'}$ .

Pair approximations for other regular lattices (see Fig. 1b-d) follow the same lines and differ only in the connectivity of  $A$  and  $B$ . Note, however, that pair approximation does not take corrections into account arising from loops. In particular, this affects the common neighbours of  $A$  and  $B$  on hexagonal and square lattices with  $N = 8$  neighbours.

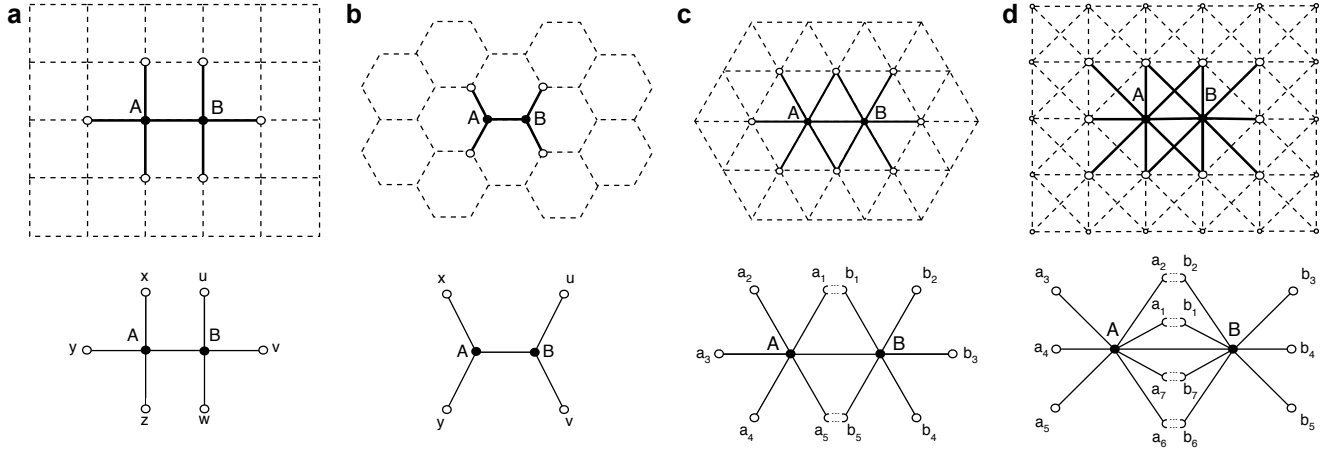
Generally, predictions by pair approximation are less reliable near the extinction thresholds of cooperators or defectors. The intuitive reason for this is that near these thresholds, effects of local correlations are more pronounced and therefore loop corrections become increasingly important.

## Alternative update rules

The update rules discussed in the main text represent a generalization of the replicator dynamics that aims at maximal consistency of spatial games with their well-mixed counterparts. This extension can be applied to any population structure. In order to demonstrate the robustness of our main results we consider multiple individuals that simultaneously compete for the colonization of a given site as well as alternative update rules that have been suggested in the literature and that incorporate different approaches to model the odds of successful reproduction of competing individuals.

### Competing with multiple individuals simultaneously

Whenever a site  $\mathbf{x}$  is updated, the present occupant and *all* its  $N$  neighbours compete for recolonizing  $\mathbf{x}$  with their offspring, which inherits the parental strategy. As in the main text, the competitive success of neighbour  $\mathbf{y}$  is determined by its payoff  $P_y$  and the transition probability  $w_y = f(P_y - P_x) \in [0, 1]$ . Given  $w_y$  for all neighbours, the occupant of the focal site  $\mathbf{x}$  succeeds in placing its offspring at  $\mathbf{x}$  with probability  $p_x = \prod_y (1 - w_y)$ . With probability  $1 - p_x$  one of the neighbouring



**Figure 1:** Four lattice configurations (top row) and the corresponding schemes used for the pair approximation with focal sites  $A$  and  $B$  (bottom row). These schemes are used to determine changes in the pair configuration probabilities  $p_{A,B \rightarrow B,B}$ . **a** square lattice with  $N = 4$  neighbours, **b** triangular lattice ( $N = 3$ ), **c** hexagonal lattice ( $N = 6$ ) and **d** square lattice ( $N = 8$ ). Note that on hexagonal and square ( $N = 8$ ) lattices, the edges from  $A$  and  $B$  to their common neighbours are considered to be independent, i.e., all corrections arising from loops are neglected.

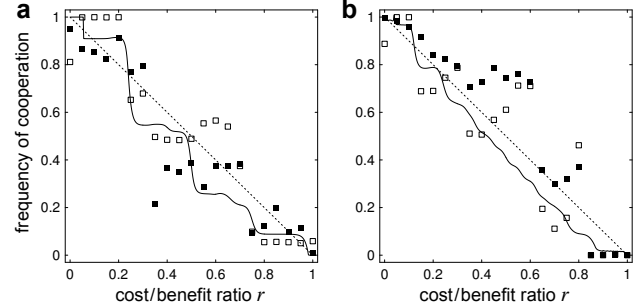
offspring takes over  $x$  with relative probabilities  $w_y/w$ , where  $w = \sum_y w_y$ .

The results obtained for the spatial Snowdrift game (not shown) are almost indistinguishable from Fig. 1 in the main text. For the continuous strategies in the spatial Hawk-Dove game the more pronounced spatial correlations, arising from the simultaneous competition with all neighbors, result in a slight decrease of dove-like behaviour for synchronous updating, but in an increase for asynchronous updating; this increase tends to be greater for large  $r$  and is at most 25%.

**Best-takes-over** This is a deterministic rule according to which the individual with the highest payoff in a given neighbourhood reproduces with certainty. It is important to note that this rule does not reduce to the replicator dynamics when applied to individual-based models of populations without spatial structure.

Technically, this rule is particularly simple to implement, but its biological relevance is rather limited because it assumes a noise free environment. The lack of stochasticity also magnifies the importance of certain local configurations, which results in discontinuous jumps and plateaus of the steady state frequency of cooperators as a function of the cost-to-benefit ratio  $r$ . The lack of stochasticity also prevents a proper equilibration process, so that steady state frequencies of cooperators and defectors depend on the initial configuration. This is true for both synchronous and asynchronous updating of the population. Moreover, this rule implies that the probability of taking over is a step function, and this discontinuity leads to numerical difficulties when solving the analytical pair approximation. To avoid these difficulties, the step function was approximated by  $f(z) = (1 + \exp(z/\kappa))^{-1}$  for suitably small  $\kappa = 0.01$  in the pair approximation (solid line in Figs. 2a,b).

Figs. 2a,b show that enhancement and inhibition of cooperation in the Snowdrift game due to spatial structure occur similarly often and without distinct patterns for synchronous and asynchronous updating. The larger number of neighbours

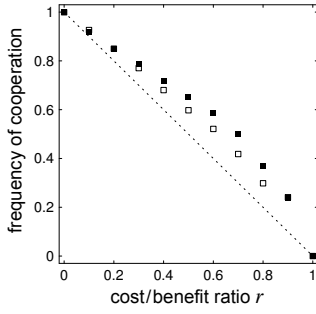


**Figure 2:** Frequency of cooperators as a function of the cost-to-benefit ratio  $r = c/(2b - c)$  in the Snowdrift game on square lattices for *best-takes-over* and different neighbourhood sizes  $N$ : **a**  $N = 4$  and **b**  $N = 8$ . The frequency of cooperation sensitively depends on  $r$  for both synchronous (*closed squares*) and asynchronous (*open squares*) population updates. At the same time it is quite impossible to derive clear trends as compared to well-mixed populations (*dotted line*). Predictions by pair approximation (*solid line*) are rather poor but at least the numerous jumps and plateaus are qualitatively reproduced. See methods for simulation details.

in Fig. 2b leads to an increase in the number of discontinuous transitions in the frequency of cooperators and produces slightly smoother results.

In the spatial Hawk-Dove game with mixed strategies, evolution occurs through a series of favourable mutations, i.e. small changes in strategies. For *best-takes-over* the simulation results are close to those expected for well-mixed populations, although spatial structure slightly favours cooperation (Fig. 3).

**Proportional updating** This is a stochastic rule where a focal individual and all its neighbours compete for reproduction. Each contestant  $i$  successfully reproduces with a probability  $p_i = P_i / \sum_j P_j$  where  $P_i$  denotes the payoff of  $i$  and the sum runs over all  $N$  contestants. For well-mixed populations, this



**Figure 3:** Average mixed strategy at stochastic equilibrium in the spatial Hawk-Dove game for *best-take-over*. Results are shown for synchronous (*closed squares*) and asynchronous (*open squares*) updating. For details see Fig. 5, methods and text.

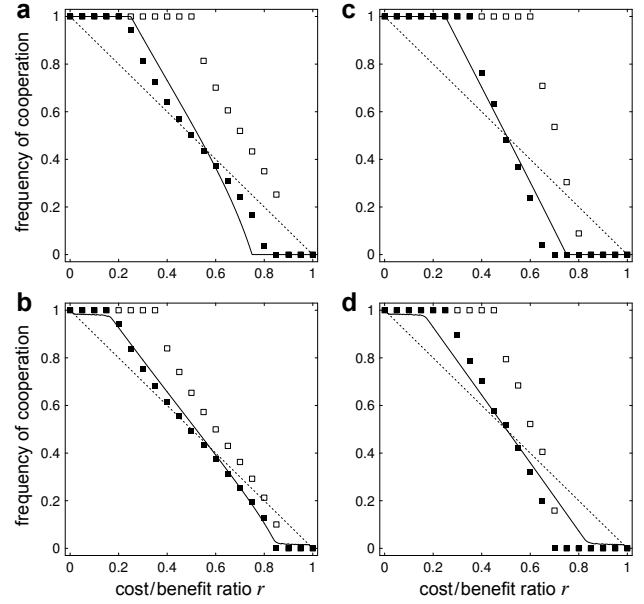
rule again does not reduce to the replicator dynamics and moreover it is ill defined for games with negative payoffs such as the Hawk-Dove game in its classical formulation. The latter problem can be resolved by adding a constant  $\alpha$  to all payoffs, but there is no 'canonical' way to determine  $\alpha$ . In contrast to the replicator dynamics and generalizations thereof, which are based on payoff differences, adding different  $\alpha$  affects the dynamics of the system. In particular, if  $\alpha \gg 0$  reproductive selection becomes random, i.e.  $p_i \rightarrow 1/N$ . The increased stochasticity could be interpreted in terms of noise, but there is no natural way to define its scale.

With proportional updating considerable differences occur for synchronous and asynchronous updates (Fig. 4): The additional noise of asynchronous updating favours cooperators and spatial structure becomes detrimental for cooperation only around  $r = 0.8$ . Increases in the neighbourhood size diminish effects of spatial structure and approach the results for well-mixed populations. In contrast, increases in  $\alpha$  amplify random fluctuations which facilitate the elimination of either strategy. This reduces the transition region where cooperators and defectors co-exist and result in more abrupt changes from all cooperation to all defection.

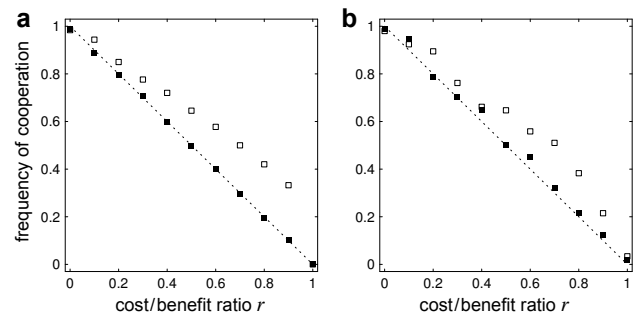
For mixed strategies in the spatial Hawk-Dove game (Fig. 5), the strategies present in the population at any one point in time only differ slightly and therefore have very similar payoffs. The small payoff differences largely eliminate deterministic competition and result in an almost random selection of reproducing individuals which results in a severe slowdown of the simulations for proportional updating. Larger  $\alpha$  further increase these effects. To compensate, the number generations before measuring the average mixed strategy was increased to  $2 \cdot 10^4$ .

As compared to the results presented in the main text, proportional updating (Fig. 4) slightly favours dove-like behavior, such that for synchronous updating the average equilibrium strategy is close to expectations from well-mixed populations, and for asynchronous updating spatial structure slightly promotes dove-like behavior beyond the corresponding levels in well-mixed populations - to a similar degree as in the case with simultaneous competition among multiple individuals discussed above. For large  $\alpha$  (Fig. 4b,c) the increased noise in the system is reflected in larger variation in the results and tends to obliterate effects of spatial structure.

Further model variations, e.g. in lattice geometry or update rules, can be investigated using the on-line material at <http://www.univie.ac.at/virtuallabs>.



**Figure 4:** Frequency of cooperators as a function of the cost-to-benefit ratio  $r = c/(2b - c)$  in the Snowdrift game on square lattices with proportional updating and different neighbourhood sizes  $N$ : **a, b**  $\alpha = 0$ ,  $N = 4$  and  $N = 8$ ; **c, d** ditto for  $\alpha = 10$ . For both synchronous (*closed squares*) and asynchronous (*open squares*) population updates the same patterns are observed as in the main text: for small  $r$  spatial structure promotes cooperation but favours defection for large  $r$ . Pair approximation correctly predicts these tendencies, but fits the synchronous results better than the asynchronous ones, despite the fact that pair approximation is based on the assumption of continuous time, and hence on asynchronous updating. The width of the transition region is conversely affected by increasing  $N$  and  $\alpha$ : while larger  $N$  widen the region, larger  $\alpha$  steepen the transition. See methods for simulation details.



**Figure 5:** Average mixed strategy at stochastic equilibrium in the spatial Hawk-Dove game on square lattices with  $N = 4$  neighbours as a function of the parameter  $r = \beta/\gamma$ . For proportional updating spatial structure generally has little effect on the frequency of dove-like behaviour: **a** for  $\alpha = 0$  and **b**  $\alpha = 10$ . Results are shown for synchronous (*closed squares*) and asynchronous (*open squares*) updating. See methods and text for simulation details.