Supplementary information for

Resource heterogeneity can facilitate cooperation

Ádám Kun[1,2,3,4*] & Ulf Dieckmann[1]

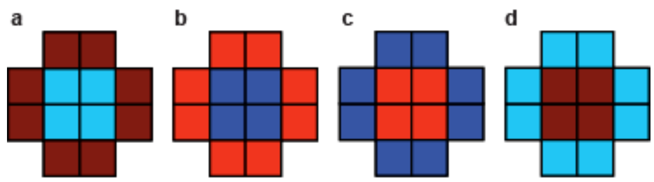
[1] Evolution and Ecology Program, International Institute for Advanced System Analysis, Schlossplatz 1, A-2361 Laxenburg, Austria

[2] Parmenides Center for the Conceptual Foundations of Science, Kirchplatz 1, D-82049 Munich/Pullach, Germany

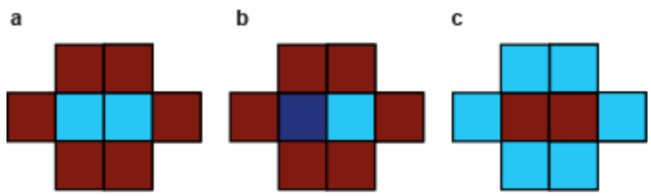
[3] Department of Plant Systematics, Ecology and Theoretical Biology, Institute of Biology, Eötvös University, Pázmány Péter sétány 1/C, 1117 Budapest, Hungary

[4] Research Group of Theoretical Biology and Evolutionary Ecology, Eötvös University and The Hungarian Academy of Sciences, Pázmány P. sétány 1/C, H-1117 Budapest, Hungary

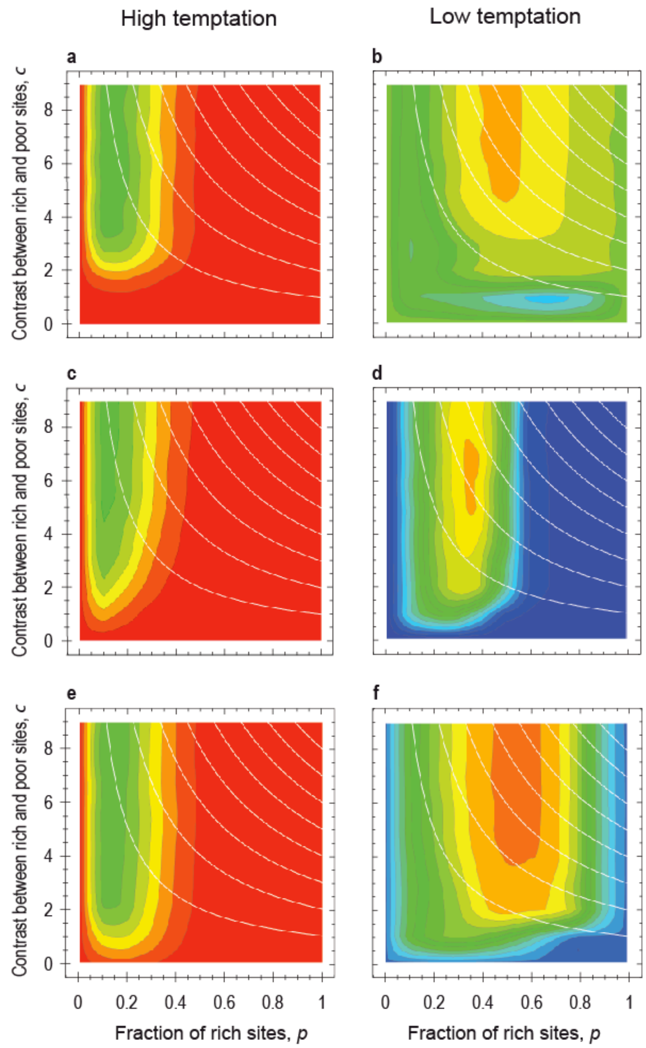
[*] To whom correspondence should be addressed:
Email: kun@iiasa.ac.at
Address: Evolution and Ecology Program, International Institute for Advanced System Analysis, Schlossplatz 1, A-2361 Laxenburg, Austria
Phone: +43 2236 807 604
Fax: +43 2236 807 466



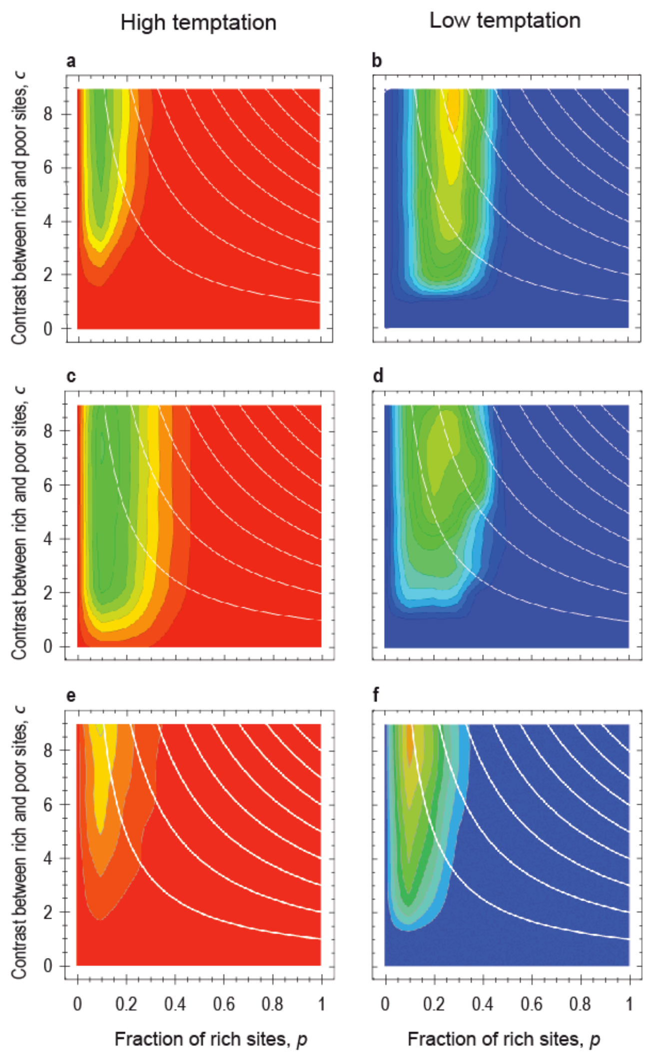
Supplementary Figure S1 | Fundamental clusters of 2×2 players that behave differently in heterogeneous and homogeneous environments. In a homogeneous environment, configurations **a-b** and also **c-d** become identical. In a homogeneous environment a cluster of 2×2 cooperators can only grow if $b < 1.25$, and a cluster of 2×2 defectors can be eliminated if $b < 1.25$. In a heterogeneous environment configuration (**a**) can grow if $1.25 > b/(c+1)$ whereas configuration (**b**) cannot grow if $1.25 < b(c+1)$. Similarly, clusters of defectors (**c-d**) behave differently in heterogeneous environment as configuration (**c**) cannot be eliminated if $1.25 < b(c+1)$, but can be eliminated if $1.25 > b-c$. Cooperators are indicated by blue colouring and defectors by red colouring. Brighter colours indicate rich sites.



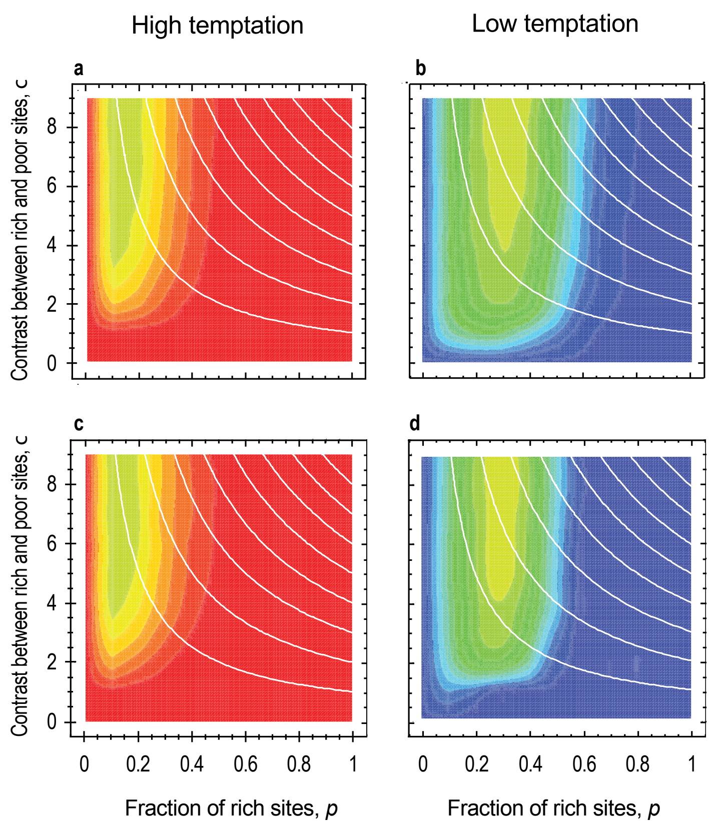
Supplementary Figure S2 | Fundamental clusters of 2×1 players that behave differently in heterogeneous and homogeneous environments. In a homogeneous environment, configurations **a**-**b** become identical. Cooperators in configuration **a**-**b** cannot grow in a homogeneous environment, whereas in heterogeneous environment such configurations can grow if and only if (**a**) $c+1>b$ or (**b**) $c/4>b-1$ (poor cooperator) and $3c/4>b-1$ (rich cooperator). Pair of defectors (**c**) cannot be eliminated in a homogeneous environment, whereas they can be eliminated in a heterogeneous environment if and only if $c+1>b$. Colors as in Supplementary Fig. S1.



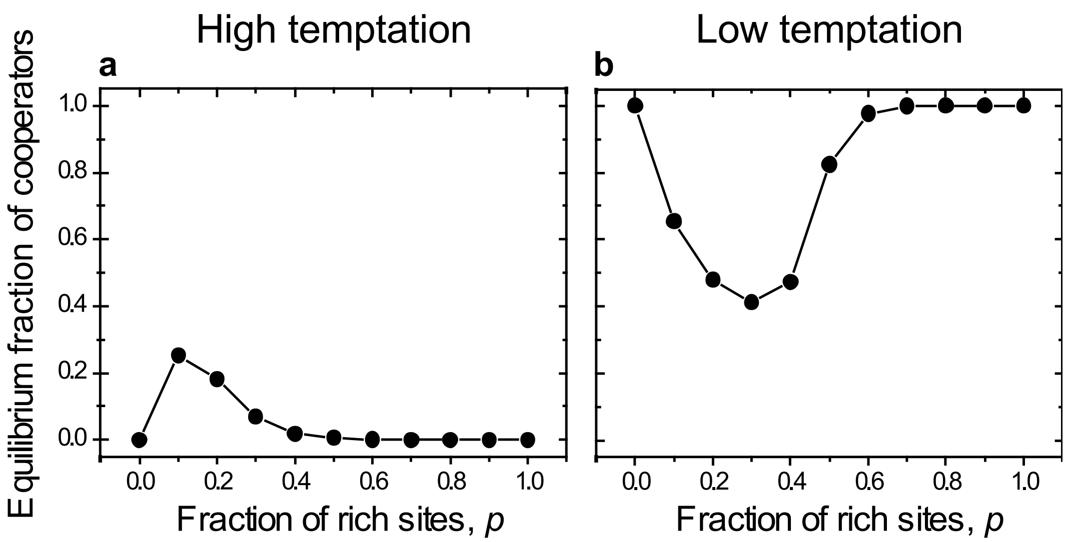
Supplementary Fig. S3 | Equilibrium fraction of co-operators as a function of the fraction p of rich sites and the contrast c between rich and poor sites. Equilibrium fraction of co-operators is shown after 5×10[8] steps. (**a**,**b**) Asynchronous deterministic updating, (**c**,**d**) synchronous stochastic updating, and (**e**,**f**) synchronous deterministic updating. Panels depict the fraction of cooperators through a colour scale from 0 (red) to 1 (blue), based on 10 (**a**, **c**, **e**) or 40 (**b**, **d**, **f**) independent model runs with increments of 0.1 in p and of 1 in c. Initial strategies are set at random, with a 0.5 fraction of cooperators. White lines represent iso-wealth curves: along these, the average resource level of sites, $pR_2 + (1-p)R_1$, remains constant. Other parameters: $m = 10$ and $b - 1 = 0.7$ (high temptation; **a**, **c**, **e**) or $b - 1 = 0.1$ (low temptation; **b**, **d**, **e**).



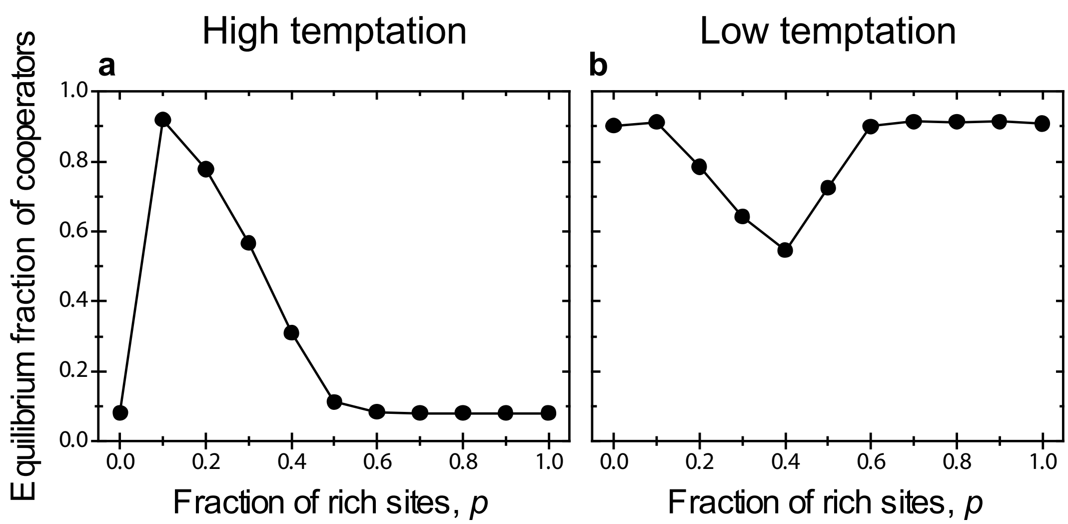
Supplementary Fig. S4 | Equilibrium fraction of cooperators on different interaction structures. Results are for (**a**,**b**) a lattice with Moore neighborhood, (**c**,**d**) a random regular graph, or (**e**,**f**) a scale-free graph. Other details as in Supplementary Fig. S3.



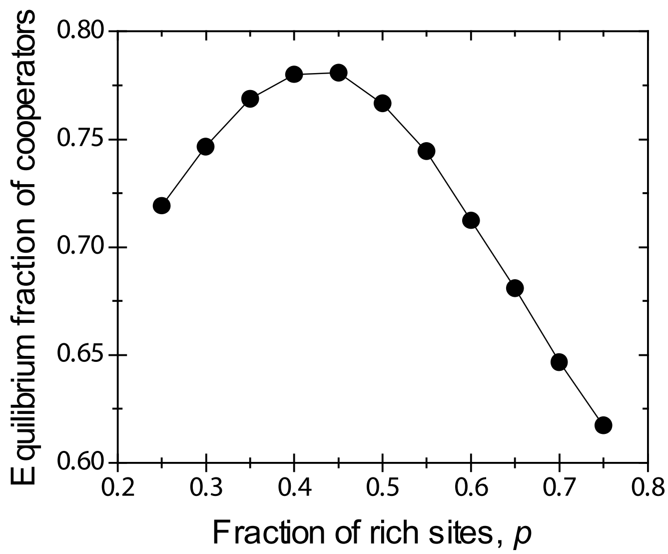
Supplementary Figure S5 | Equilibrium fraction of cooperators when players can err. Either all players can err, i.e. cooperators defect and defectors cooperate (**a**,**b**) or only cooperators can err, i.e. behave as defectors (**c**,**d**). Other details as in Supplementary Fig. S3.



Supplementary Figure S6 | Equilibrium fraction of cooperators with continuous levels of resources as a function of the fraction p of rich sites. Resources are either low, $R_1 + \rho = 1 + \rho$, or high, $R_2 + \rho = 9 + \rho$, where ρ is a random number drawn from a Gaussian distribution with mean 0 and standard deviation $\sigma = 0.5$. Other parameters: $m = 10$, and $b = 1.7$ (high temptation; **a**) or $b = 1.1$ (low temptation; **b**).



Supplementary Figure S7 | Equilibrium fraction of cooperators in a 5-player Public Good Game as a function of the fraction p of rich sites. Equilibrium fraction of co-operators is shown after $5{\times}10^8$ steps. Other parameters: $m = 10$ and $r = 1.05$ (high temptation; **a**) or $r = 1.2$ (low temptation; **b**).



Supplementary Figure S8 | Equilibrium fraction of co-operators in the Heterogeneous Snowdrift Game, as a function of the fraction p of rich sites. Equilibrium fraction of co-operators is shown after 5×10^8 steps. The mean benefit of cooperation is kept constant, $B = 1.5$. Other parameters: $m = 10$ and $d = 0.5$.

Supplementary Table S1 | Quantitative descriptors of the results.

High temptation	Equilibrium fraction of cooperators		Fraction of rich sites	
	Minimum	Maximum	At maximum	Range around maximum
Asynchronous stochastic updating	0	0.25	0.01	0.01 – 0.42
Asynchronous deterministic updating	0	0.31	0.08	0.01 – 0.45
Synchronous stochastic updating	0	0.30	0.01	0.01 – 0.51
Synchronous deterministic updating	0	0.31	0.01	0.01 – 0.44
Moore neighbourhood	0	0.32	0.02	0.01 – 0.18
Interactions on random regular graphs	0	0.37	0.01	0.01 – 0.52
Interactions on scale-free graphs	0	0.20	0.01	0.01 – 0.27
Errors in strategy execution (both can err)	0	0.32	0.02	0.01 – 0.40
Errors in strategy execution (only cooperators can err)	0	0.32	0.01	0.01 – 0.40

Low temptation	Equilibrium fraction of cooperators		Fraction of rich sites	
	Minimum	Maximum	At minimum	Range around maximum
Asynchronous stochastic updating	0.43	1	0.39	0.08 – 0.58
Asynchronous deterministic updating	0.27	0.62	0.56	0.01 – 0.99
Synchronous stochastic updating	0.34	1	0.45	0.09 – 0.53
Synchronous deterministic updating	0.21	0.77	0.59	0.01 – 0.99
Moore neighbourhood	0.38	1	0.37	0.05 – 0.43
Interactions on random regular graphs	0.50	1	0.35	0.02 – 0.45
Interactions on scale-free graphs	0.59	1	0.19	0.02 – 0.34
Errors in strategy execution (both can err)	0.38	1	0.44	0.01 – 0.67
Errors in strategy execution (only cooperators can err)	0.44	1	0.40	0.01 – 0.60

Equilibrium fraction of cooperators at both high and low temptation is given. Maximums and minimums are extracted from the primary data. The maximum (minimum) is further characterized by the fraction of rich site at it, estimated by interpolating the primary data by fitting a polynomial (6th order). Furthermore, the range of fraction of rich sites in which the fraction of cooperators are higher (lower) by more than 5% compared to the one observed in homogeneous environment is also shown.

Supplementary Note 1: PDS analyses

Here we first introduce the notion of configurations comprising a fixed number of sites. We then describe how we rank these configurations according to their prevalent-deviation score (PDS), which gives critical insights into the mechanism underlying our results.

Configurations. There are $2^4 = 16$ possible combinations of site pairs when considering all possible configurations of site strategy (cooperator or defector) and site quality (rich or poor). After accounting for symmetries (rotations and reflections) among these 16 configurations, only 10 remain. Likewise, after accounting for symmetries, there are 80 3-site configurations, 785 4-site configurations, and 8620 5-site configurations. When considering only the shapes of these configurations, they are known as polyominos[61]: there are 6 3-site polyominos (trominos), 19 4-site polyominos (tetrominos), and 63 5-site polyominos (pentominoes).

Prevalent-deviation scores. Based on the observed frequency of cooperators and the know frequency *p* of rich sites, we calculate the expected frequency $\hat{f}$ of each configuration expected when sites are distributed independently and randomly. Comparing this with a configuration's actual frequency f, the prevalent-deviation score (PDS) is calculated as $f \log_{10}(f / \hat{f})$. It thus measures both the deviation from the expected frequency of a configuration and the prevalence of that configuration. In other words, only those configurations will have a high PDS that are both prevalent and exhibit a high deviation. It is these configurations that are expected to play the largest role in creating deviations in heterogeneous environment relative to homogeneous environment.

For the PDS analyses reported here, we choose two parameter combinations, one for high temptation and one for low temptation (see caption of Fig. 3), for which the effects of heterogeneity are large. Note that our definition of the PDS shares some similarities with that of Kullback-Leibler divergence[62].

Results of PDS analyses. Comparing the PDS of all configurations involving 2, 3, 4, or 5 players reveals that configurations with high PDS (Fig. 3) have the following common characteristics: (1) Most of these configurations comprise either only cooperators or only defectors. This shows that cooperators cluster, and as a consequence of this, defectors also cluster. This phenomenon is well known in other spatial games. (2) Rich players having different strategies never (high temptation) or very rarely (low temptation) neighbour each other. Thus, rich islands are monopolized by either cooperators or defectors. (3) There is at least one rich player in the configurations comprising 3 or more sites (except in the 8th 3-site configuration at high temptation). If two rich players are part of the configuration, they always neighbour each other. Thus, small islands of rich players are surrounded by poor players having the same strategy. Together, these observations quantitatively corroborate our qualitative finding that at high temptation to defect a rich cooperator is usually found at the core of a cooperating cluster (Fig. 1).

Summary. Our PDS analyses identify configurations that are both prevalent and whose frequencies strongly deviate from what is expected for randomized configurations. Configurations with high PDS must therefore be expected to play a key role in stabilizing the observed strategy patterns. In particular, these analyses show that small rich islands monopolized by cooperators (high temptation) or defectors (low temptation) are the critical configurations responsible for the observed increased (high temptation) or decreased (low temptation) levels of cooperation.

Supplementary Note 2: Analysis of fundamental clusters

Building on the results of our PDS analyses, here we demonstrate analytically how the game dynamics around small rich islands is qualitatively altered by environmental heterogeneity.

Fundamental clusters. Hauert[25] investigated spatial games by introducing the notion of fundamental clusters. A fundamental cluster is the smallest configuration that, if it can grow initially, will continue to grow indefinitely, thus guaranteeing the spread of the strategy it harbours. Hauert concluded that for the von Neumann neighbourhood with synchronous deterministic updating all fundamental clusters are 2×2 clusters so that "if the growth criteria for 2×2 clusters hold… the strategy is able to invade a world of opponents and survive forever"[25].

2×2 clusters in homogeneous environments. In a homogeneous environment the fundamental cluster given by a 2×2 block of four cooperators (Supplementary Fig. S1, with the first two and also the last two panels becoming identical) grows if and only if $2 > b + 3(b-1)$ (homogeneous poor environment) or $2c + 2(2c+1) > (bc + b + c) + 3(bc + b - 1)$ (homogeneous rich environment), which both reduce to $b < 1.25$. Similarly, a 2×2 block of four defectors will be eliminated (because surrounding cooperators have higher payoffs) if and only if $3 > 2b + 2(b-1)$ (homogeneous poor environment) or $c + 3(2c+1) > 2(bc + b + c)$ $+2(bc + b - 1)$ (homogeneous rich environment), which again both reduce to $b < 1.25$.

The value $b = 1.25$ of the temptation to defect thus is the critical value separating temptations for which cooperators dominate ($b < 1.25$) or disappear ($b > 1.25$) in a homogeneous environment. It is also the critical value separating temptations for which environmental heterogeneity hinders (low temptation) or helps (high temptation) cooperation.

2×2 clusters in heterogeneous environments. Here we extend the work of Hauert[25] to 2×2 clusters in heterogeneous environments, which are depicted in Supplementary Fig. S1.

Cooperators can grow in cluster (a) if and only if $1.25(c+1) > b$, which, for example, is satisfied for $b = 1.7$ if $c > 0.36$. As shown above, cooperators cannot grow in such a configuration in a homogeneous environment, if the temptation to defect is high ($b > 1.25$). However, in a heterogeneous environment, this cluster of cooperators can expand, given small to medium contrast c.

Cooperators in cluster (b) can grow if and only if $1.25 > b(c+1)$, which even at $b = 1$ requires $c < 0.25$. Thus, for the parameters in Fig. 2, this cluster cannot grow at low temptation ($b < 1.25$), even though the analogous cluster can grow in a homogeneous environment (see above).

Defectors will be eliminated in cluster (c) if and only if $1.25 > b(c+1)$ (conservatively assuming poor cooperators in the surrounding). The inequality cannot be satisfied at low temptation ($b < 1.25$), if contrast c is high. Cooperators in the corresponding homogeneous configuration will eliminate the defectors at low temptation, whereas in a heterogeneous environment they cannot do so even for very small contrast, c.

Defectors will be eliminated in cluster (d) if and only if $1.25 + c > b$ (assuming rich cooperators in the surrounding) or $1.25 + c/2 > b$ (conservatively assuming poor cooperators in the surrounding). In the corresponding homogeneous configuration, the defectors cannot be eliminated at high temptation, whereas this will occur in a heterogeneous environment.

2×1 clusters in homogeneous environments. While Hauert[25] has shown that fundamental clusters are given by 2×2 blocks in homogeneous environments (which is why we analyzed them above also for heterogeneous environments), it turns out that in heterogeneous environment the fundamental clusters are given by 2×1 blocks (which is why we analyze these next). A pair of cooperators amidst defectors can grow if and only if $b < 1$, which by definition cannot happen. Thus, such a configuration cannot grow in a homogeneous environment, and therefore is not a fundamental cluster in that setting.

Similarly, a pair of defectors amidst cooperators cannot be eliminated in a homogeneous environment, as this would again require $b<1$.

2×1 clusters in heterogeneous environments. Two rich cooperators amidst poor defectors (Supplementary Fig. S2a) will grow if and only if $c+1>b$, and thus only if $c>0$, i.e., only in a heterogeneous environment. Furthermore, in a configuration with one of the two cooperators situated on a rich site (Supplementary Fig. S2b), the poor cooperator will grow if and only if $c/4>b-1$, and the rich cooperator will grow if and only if $3c/4>b-1$. This again demonstrates that cooperators can grow in a heterogeneous environment, even when they cannot grow in the corresponding homogeneous environment.

Two poor defectors amidst rich cooperators (Supplementary Fig. S2c) will be eliminated if and only if $c+1>b$. This is always requires a heterogeneous environment ($c>0$). Furthermore, if we assume (as the least favourable setting) that each of the six considered rich cooperators have only one other cooperative rich neighbour, while the other neighbours (save the two defector in the middle) are poor cooperators, then the defectors will be eliminated if and only if $0.5c+1>b$. Thus, this configuration of defectors cannot be eliminated in a homogeneous environment, but can be in a heterogeneous environment.

Star-shaped configurations in homogeneous environment. We finally turn to the configuration that has the highest PDS (see above), which is star-shaped (Fig. S3g, rank 1). This configuration consists of five cooperators, one in the centre, and one neighbouring it on each of the four sides. The later cooperators have one cooperative and three defective neighbours. Those surrounding defectors could have as many as two cooperative neighbours (this is true for the 4 defectors residing in the four indentations of the star). The cooperators can achieve a higher payoff than these defectors, and therefore grow, if and only if $3/4>b$, which can never be satisfied, as $b>1$ by definition. Thus, such a configuration cannot grow in a homogeneous environment.

Star-shaped configurations in heterogeneous environments. In a heterogeneous environment, we focus on a star-shaped configuration consisting of a rich cooperator neighboured by four poor cooperators (Fig. S3g, rank 1). Now, the poor cooperators have higher payoffs than any of the surrounding poor defectors, and will thus grow if and only if $c/4+1>b$, which can always be fulfilled in a sufficiently heterogeneous environment.

Summary. We have shown that in heterogeneous environments a 2´1 block of rich cooperators amidst poor defectors is a fundamental cluster. Its capacity to grow in heterogeneous high-temptation environments allows the persistence of cooperation. Similarly, a 2´2 block of rich defectors amidst poor cooperators perseveres in heterogeneous low-temptation environments, thereby allowing the persistence of defection. These analytical findings for synchronous deterministic updating are fully in line with what we observe for asynchronous stochastic updating.

Supplementary References

61. Golomb, S. W. *Polyominoes (2nd ed.)*. (Princeton Univ. Press, 1994).

62. Kullbach, S. & Leibler, R. A. On information and sufficiency. *The Annals of Mathematical Statistics* **22**, 79–86 (1951)