in patch $r$ when it wins against its subordinate strategy, and $-c_i^r$ (i.e. the cost to the loser) be the payoff to strategy $i$ in patch $r$ when it loses against the dominant strategy. Under these assumptions, the payoff matrix in patch $r$ is given by

$$\mathbf{A}(r) = a^r + \begin{pmatrix} 0 & -c_1^r & b_1^r \\ b_2^r & 0 & -c_2^r \\ -c_3^r & b_3^r & 0 \end{pmatrix}. \quad (3)$$

Throughout this article, we assume that $a^r > 0, 0 < c_i^r < a^r, b_i^r > 0$. The assumption $a^r > c_i^r$ ensures that payoffs remain positive.

### 2.2. Analytical and numerical methods

To understand whether the strategies persist in the long term, we analyze (2) using a combination of analytical and numerical methods. Long-term persistence of all the strategies is equated with *permanence*: there exists a minimal frequency $\rho > 0$ such that

$$x_i^r(t) \geq \rho \quad \text{for all } i, r$$

whenever $t$ is sufficiently large and all strategies are initially present (i.e. $\sum_r x_i^r(0) > 0$ for $i = 1, 2, 3$). Permanence ensures that populations recover from rare large perturbations and continual small stochastic perturbations (Schreiber, 2007; Benaïm et al., 2008). Using analytical techniques developed by Hofbauer and Schreiber (2010), we derive an analytical condition for permanence in terms of products of eigenvalues at the single strategy equilibria of the model. These criteria take on an explicit, interpretable form when (i) populations are relatively sedentary (i.e. $d_{rr} \approx 1$ for all $r$) and (ii) populations are well mixed (i.e. there exists a probability vector $v = (v_1, \ldots, v_n)$ such that $d_{rs} \approx v_s$ for all $r, s$). To better understand permanence at intermediate dispersal rates, we derive an analytical result about critical dispersal thresholds for persistence of metacommunity exhibiting unconditional dispersal (i.e. probability of leaving a patch is independent of location) and numerically simulate (2) using the deSolve package of R (R Development Core Team, 2008). To simplify our exposition, we present our results under the assumption that $m^r = m$ and $a^r = a$ for all $r$, i.e. there is only spatial heterogeneity in the benefits and in the costs. More general results are presented in the Appendices.

## 3. Results

### 3.1. Local coexistence

We begin by studying the behavior of the within-patch dynamics (1) in the absence of dispersal. If only strategy $i$ is present in patch $r$, then the per-capita growth rate of the strategy, call it $j$, dominated by strategy $i$ is $-m\,c_i^r/a$. Alternatively, the per-capita growth rate of the strategy $j$ dominating strategy $i$ equals $m\,b_i^r/a$. The three single-strategy equilibria are connected by population trajectories in which dominant strategies replace subordinate strategies (Fig. 1). This cycle of population trajectories in patch $j$ is known as a *heteroclinic cycle* (Hofbauer and Sigmund, 1998). Using average Lyapunov functions, time-one maps, or measure-theoretic techniques (Hofbauer, 1981; Krupa and Melbourne, 1995; Schreiber, 2000), one can show that the strategies in patch $r$ locally coexist in the sense of permanence provided that the product of the invasion rates exceeds the product of the exclusion rates:

$$\prod_i b_i^r > \prod_i c_i^r. \quad (4)$$

Interestingly, inequality (4) is equivalent to the determinant of the payoff matrix being positive.

When coexistence occurs, the heteroclinic cycle of the boundary of the population state space is repelling and there is a positive global attractor for the within-patch dynamics (Fig. 1(a)). When inequality (4) is reversed, the heteroclinic cycle on the boundary is attracting (Fig. 1(b)). The strategies asymptotically cycle between three states (rock-dominated, paper-dominated, scissors-dominated), and the frequencies of the under-represented strategies asymptotically approach zero. Hence, all but one strategy goes extinct when accounting for finite population sizes.

### 3.2. Metacommunity coexistence

*Analytical results*. When the patches are coupled by dispersal, we show in Appendix A that for any pair of strategies, the dominant strategy competitively excludes the subordinate strategy. Hence, as in the case of the dynamics within a single patch, the metacommunity exhibits a heteroclinic cycle on the boundary of the metacommunity phase space.

Work of Hofbauer and Schreiber (2010) on permanence for structured populations (see Appendix B) implies that metapopulation persistence is determined by invasion rates and exclusion rates at single strategy equilibria. More specifically, consider the rock strategy equilibrium where $x_1^r = 1$ and $x_2^r = x_3^r = 0$ for all patches $r$. Linearizing the paper strategy dynamics at the rock equilibrium yields

$$\frac{dx_2^r}{dt} \approx -m\,x_2^r + m\frac{\sum_s d_{sr}(a + b_2^s)x_2^s}{\sum_s d_{sr}a}.$$

Equivalently, if $\mathbf{x}_2 = (x_2^1, \ldots, x_2^n)^T$ where $^T$ denotes transpose, then

$$\frac{d\mathbf{x}_2}{dt} \approx \left(-mI + m\Psi D^T(aI + B_2)\right)\mathbf{x}_2$$

where $I$ is the identity matrix, $\Psi$ is the diagonal matrix with entries $1/\sum_s d_{1s}a^s, \ldots, 1/\sum_s d_{ns}a^s$, $B_2$ is the diagonal matrix with diagonal entries $b_2^1, \ldots, b_2^n$, and $D^T$ is the transpose of the dispersal matrix. Corresponding to the fact that the paper strategy can invade the rock strategy, the stability modulus of $-mI + m\Psi D^T(aI + B_2)$ (i.e. the largest real part of the eigenvalues) is positive. Call this stability modulus $\mathcal{I}_2$, the invasion rate of strategy 2. Linearizing the scissors strategy dynamics at the rock equilibrium yields

$$\frac{d\mathbf{x}_3}{dt} \approx \left(-mI + m\Psi D^T(aI - C_3)\right)\mathbf{x}_3$$

where $C_3$ is the diagonal matrix with diagonal entries $c_3^1, \ldots, c_3^n$. Corresponding to the fact that the scissors strategy is displaced by the rock strategy, the stability modulus of $-mI + m\Psi D^T(aI - C_3)$ is negative. We call this negative of this stability modulus $\mathcal{E}_3$, the exclusion rate of strategy 3. By linearizing around the other pure strategy equilibria, we can define the invasion rates $\mathcal{I}_i$ for each strategy invading its subordinate strategy and the exclusion rates $\mathcal{E}_i$ for each strategy being excluded by its dominant strategy.

Appendix A shows that the metapopulation persists if the product of the invasion rates exceeds the product of the exclusion rates:

$$\prod_{i=1}^{3} \mathcal{I}_i > \prod_{i=1}^{3} \mathcal{E}_i. \quad (5)$$

If the inequality (5) is reversed, then the metapopulation is extinction prone as initial conditions near the boundary converge to the heteroclinic cycle and all but one strategy is lost regionally. While inequality (5) can be easily evaluated numerically, one cannot, in general, write down a more explicit expression for this permanence condition. However, when the metapopulation



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