



## Movement patterns, social dynamics, and the evolution of cooperation

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### ARTICLE INFO

#### Article history:

Received 16 December 2011

Available online 30 March 2012

#### Keywords:

Mobility  
Dispersal  
Random walks  
Game theory  
Agent-based  
Dynamic networks

### ABSTRACT

The structure of social interactions influences many aspects of social life, including the spread of information and behavior, and the evolution of social phenotypes. After dispersal, organisms move around throughout their lives, and the patterns of their movement influence their social encounters over the course of their lifespan. Though both space and mobility are known to influence social evolution, there is little analysis of the influence of specific movement patterns on evolutionary dynamics. We explored the effects of random movement strategies on the evolution of cooperation using an agent-based prisoner's dilemma model with mobile agents. This is the first systematic analysis of a model in which cooperators and defectors can use different random movement strategies, which we chose to fall on a spectrum between highly exploratory and highly restricted in their search tendencies. Because limited dispersal and restrictions to local neighborhood size are known to influence the ability of cooperators to effectively assort, we also assessed the robustness of our findings with respect to dispersal and local capacity constraints. We show that differences in patterns of movement can dramatically influence the likelihood of cooperator success, and that the effects of different movement patterns are sensitive to environmental assumptions about offspring dispersal and local space constraints. Since local interactions implicitly generate dynamic social interaction networks, we also measured the average number of unique and total interactions over a lifetime and considered how these emergent network dynamics helped explain the results. This work extends what is known about mobility and the evolution of cooperation, and also has general implications for social models with randomly moving agents.

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### 1. Introduction

In this paper, we systematically explore the effects of different random movement strategies on an archetypal model of social interaction: the evolutionary prisoner's dilemma (PD) game. Movement in humans and other animals is often modeled as a random walk, but not all random walks cover space in the same way. Research from theoretical ecology has shown that differences in random walks, as models for search strategies, can translate to large differences in foraging success, and that optimal movement behavior is dependent on the spatial distribution of resources (Bartumeus et al., 2005; Hills, 2006). When individuals must move to find partners for social interaction, differences in movement strategies change the dynamics of the *de facto* social networks describing interactions between neighbors. Models of social evolution have demonstrated an important influence of mobility – even

random movement – in the evolution of cooperation (Houston, 1993; Aktipis, 2004; Santos et al., 2006; Vainstein et al., 2007; Meloni et al., 2009). However, there is currently little work on how specific properties of random walks influence population dynamics. We show that differences in the way individuals move around can dramatically influence the likelihood of cooperator success, that these effects may be highly nuanced, and that the effects of movement differences are dependent on environmental assumptions concerning offspring dispersal and local space capacities. This work extends what is known about mobility and the evolution of cooperation, and also has general implications for social models with randomly moving agents. In addition, we connect these results to the growing literature on evolution in dynamic social networks (e.g. Pacheco et al., 2006; Santos et al., 2006; Perc and Szolnoki, 2010; Van Segbroeck et al., 2010) by assessing the explanatory role of the average numbers of total and unique agent interactions resulting from the emergent social interaction networks.

The PD game is often used to study the evolution of animal and human cooperation and altruism, and this is accomplished by identifying conditions under which cooperative strategies

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outperform defectors (Trivers, 1971; Axelrod, 1984, 1997; Nowak, 2006). In this two-player game, individuals either cooperate or defect. Defection is always the better strategy in the single-shot game, but mutual cooperation yields higher rewards than mutual defection, hence the dilemma. How cooperative strategies might succeed over selfish ones has remained a central question, and a number of mechanisms have been proposed for cooperator success, such as kin selection (Hamilton, 1963), reciprocity (Trivers, 1971; Axelrod, 1984), and limited dispersal (Hamilton, 1964) in spatially organized environments (Nowak et al., 2010).

Previous theoretical work has considered the influence of movement on the evolution of cooperation, but our approach differs from these approaches in a couple of ways. First, many models have assumed that agents are goal oriented, moving either toward cooperators or away from defectors (Dugatkin and Wilson, 1991; Enquist and Leimar, 1993; Pepper and Smuts, 2002; Aktipis, 2004; Santos et al., 2006; Helbing and Yu, 2009). In this paper, we explored the consequences for the PD game of different patterns of random movement. Different patterns of movement, as found in natural systems, can lead to different patterns of emergent assortment and interaction. Second, a number of social models, not all of which concern cooperation, have used randomly moving agents without considering the effects of the particular strategy of movement used (e.g. Bonabeau, 1997; Epstein, 1998, 2002; Pepper and Smuts, 2002; Aktipis, 2004; Panait and Luke, 2004; Beltran et al., 2006; Vainstein et al., 2007; Nonaka and Holme, 2007; de Andrade et al., 2009), and generally have not considered more than one movement strategy. We will show that, at least in the context of the evolution of cooperation (in the PD game), properties of different movement strategies matter.

While properties of random walks have not been systematically explored for models of social evolution, theoretical work on foraging models has demonstrated that different types of random walks cover space differently, and thus the effectiveness of a random walk as a search strategy depends on the spatial distribution and replenishment of resources (Bartumeus et al., 2005; Hills, 2006). Hills (2006) considered agents using correlated random walks to forage in a continuous space, and allowed the distribution of turning angles to vary. When resources were distributed in localized patches, agents did best by initially restricting their turning angle, using a highly correlated walk to explore more space, and then using much less correlated walk to remain in the same local vicinity until most of the patch's resources had been found. When many mobile individuals interact, their movement strategies dictate not only how they find static resources, but also each other. Random movement strategies can therefore have complex and non-obvious effects when individuals interact in structured environments. As an example, de Jager et al. (2011) recently found that Lévy walks, but not Brownian walks, explained the patterns of aggregation seen in populations of mussels. In the context of human social dynamics, a recent study of spatial mate choice models showed that different random walk strategies not only affected population-level statistics, including inter-pair correlations and marriage age hazard curves, but also did so differently for different individual decision rules (Smaldino and Schank, 2012). A more detailed look at random movement strategies for social models is therefore warranted.

We studied an agent-based model in which agents move randomly to find co-players, accumulate resources through PD game payoffs, and reproduce by creating a new individual with the same game and movement strategies. The ability to accumulate resources tends to favor cooperation when cooperators can assort, as consistent mutual cooperation can outperform the exploitation of cooperators by defectors if defectors' interactions with cooperators are more sporadic (Axelrod, 1984; Aktipis, 2004; Chadeaux and Helbing, 2010; Smaldino, 2011). Our model is

similar to previous work of this type (Epstein, 1998; Aktipis, 2004, 2006; Smaldino, 2011), and is novel primarily in the consideration of multiple random movement strategies. Moreover, we allowed defectors and cooperators to use different random movement strategies. This is important because the interests of these two types of individuals are opposed: defectors do best in the company of cooperators, cooperators do worst in the company of defectors. Different movement strategies generate different patterns of interactions for cooperators and defectors, and the nature of the social networks that emerge are therefore a function of individual movement strategies and their interactions with other environmental factors, such as dispersal and local space constraints. We will show that differences in agent mobility dramatically influence cooperative outcomes.

### 1.1. Limited dispersal and local neighborhood constraints

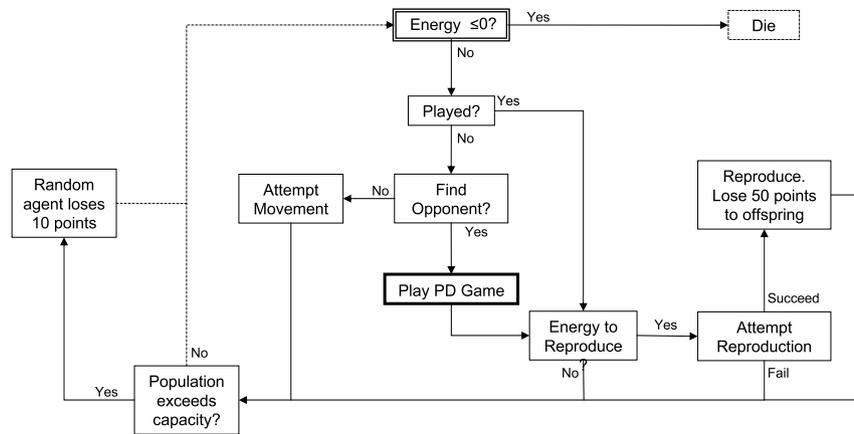
In the absence of complex cognitive or behavioral strategies, spatial organization allows cooperators to assort and form clusters in which mutual cooperation lets them outcompete defectors (Van Baalen and Rand, 1998; Killingback et al., 1999; Nowak et al., 2010) because the spatial association of cooperators allows them to play each other more than neighboring defectors. In spatially organized environments, limited dispersal – in which offspring remain close to their parents (who play the same strategy as them) – promotes the evolution of cooperation by reinforcing the spatial assortment of strategic phenotypes (Hamilton, 1964; Koella, 2000; Kummerli et al., 2009). Koella (2000) showed this with particular clarity, additionally demonstrating that when dispersal is allowed to co-evolve with cooperation, defectors should evolve longer-range dispersal and thereby curb the growth of more closely-dispersing cooperators.

In previous spatial models (Koella, 2000; Mitteldorf and Wilson, 2000; Számadó et al., 2008), individuals remained stationary after their initial dispersal, so that local neighborhoods changed only through the death and birth of neighbors. With the additional assumption of mobility, individual neighborhoods will change as organisms move around. Mobility is known to affect the success of cooperative strategies. For example, cooperators do well when individuals actively move away from defectors or seek out cooperative neighbors (Pepper and Smuts, 2002; Aktipis, 2004; Santos et al., 2006; Helbing and Yu, 2009), while highly mobile defectors may exploit relatively stationary cooperators (Dugatkin and Wilson, 1991; Enquist and Leimar, 1993). The ability of cooperators to resist defectors, however, may depend on local restrictions on neighborhood size: if defectors can always follow cooperators to new neighborhoods, defectors will continue to exploit those cooperators (Pepper, 2007; Smaldino and Lubell, 2011).

Exactly how both limited dispersal and local capacity constraints interact with mobility is not well understood. To this end, we varied environmental assumptions concerning these two factors, allowing dispersal to be either limited or random and local capacities to be either finite or unlimited.

### 1.2. Modeling cooperation with mobile agents

We studied an agent-based model in which mobile agents played the PD game with neighbors and moved when unable to find a co-player. We explored differences in mobility by defining a class of random walk strategies on a discrete square lattice, which is a common context for agent-based investigations in the biological and social sciences. We allowed cooperators and defectors to use different movement strategies, and kept the probability of movement constant for all individuals, focusing instead on the degree to which the random walks were exploratory or restricted in their coverage of space. Dispersal was limited in



**Fig. 1.** Flowchart depicting an agent's activity cycle. The first action is to check whether the agent has enough energy to continue living, indicated in double-line outline.

the initial model in order to focus on differences in movement strategies. While previous theory indicates that cooperators benefit by staying close to one another and that defectors benefit by roaming widely, the exact nature of this relationship remains unknown. To investigate the latter questions more deeply, we studied the influences of two environmental assumptions: limited dispersal and restricted local capacity.

## 2. Model description

In this model, mobile agents were situated on a square lattice, played the PD game with neighbors, and attempted movement when unable to find a co-player. Each game encounter represented an opportunity to gain resources in the form of energy units. If an agent gained enough energy, it attempted to reproduce. If its energy fell to zero, it died. Individuals played pure strategies of cooperate or defect, and produced offspring of the same type.

Agents were scheduled asynchronously using the MASON simulation environment (Luke et al., 2005), so that the order of scheduling was randomized at each time step. Each simulation began with 50 cooperators and 50 defectors placed in unique, random locations, and initialized with an energy level drawn from a uniform distribution of integers between 1 and 50. Following Aktipis (2004), the population size was kept in check by deducting 10 energy units from a random agent whenever the population exceeded the environmental carrying capacity of 100 agents. Interactions took place on a  $25 \times 25$  square grid with periodic (toroidal) boundaries. Model runs proceeded in discrete time steps ("rounds"). During each round, every agent went through an activity cycle, diagrammed in Fig. 1.

At the beginning of a round, if the agent's energy had fallen to zero, it died and was removed from space. If the agent did not die and it had not already played the PD game that round (having been the co-player of a previously scheduled agent), it searched its local neighborhood for a co-player who had also not already played that round. An agent's local neighborhood consisted of the eight closest cells (its Moore neighborhood). If the agent found a co-player, the two played the PD game and received payoffs. The payoffs used were  $DC = 5$ ,  $CC = 3$ ,  $DD = 0$ ,  $CD = -1$ , where the first letter denotes the game strategy used by the player of interest, and the second letter denotes the game strategy of its co-player.

If a co-player could not be found, the agent attempted to move using its random walk strategy, described below. Movement attempts were not always successful; agents could not occupy the same location, so a move attempt could fail if another agent occupied the cell the agent attempted to move into—we refer to this restriction as a *finite local capacity*. There was no cost associated with movement, other than the lack of an opportunity to gain energy payoffs from a game interaction.

If the agent reached 100 energy units, it attempted to reproduce into a random cell in its local neighborhood, providing 50 of its energy units to its offspring. If the random cell was occupied, the agent did not reproduce.

Our model is similar to the Walkaway model of Aktipis (2004), with several differences. First, movement was never contingent on previous game outcomes; all agents were "naïve", and moved only in the absence of an available co-player. Second, multiple agents could not occupy the same location (cf. Vainstein et al., 2007; Epstein, 1998). If an agent attempted to move to or reproduce into a currently occupied location, the action was unsuccessful. Third, since agents could not occupy the same location, game partners were chosen from the eight neighboring cells, rather than among co-occupants of the same cell. Fourth, reproduction was spatially correlated. Offspring were reproduced near their parents instead of in a random location in space. Finally, we considered several random walk strategies, and allowed cooperators to move differently from defectors. As mentioned, the assumptions of a finite local capacity and limited dispersal were altered for certain analyses; these changes are described in greater detail below.

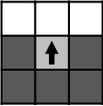
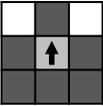
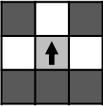
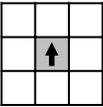
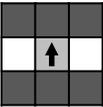
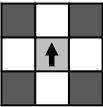
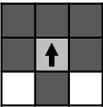
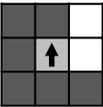
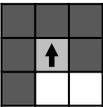
### 2.1. Random movement strategies

Consider an agent on a square lattice, with an orientation toward one of its eight neighboring cells. The agent can be thought of as "facing" one of its neighboring cells, so that a move "forward" one step will place the agent in that cell. When the agent moves to a new cell, its orientation is updated to the direction from its previous location to its current location. For example, if the agent moves to its forward-right, its new orientation will be 45 degrees clockwise from its previous heading. We considered the class of random walks defined by allowing a subset of (oriented) neighboring cells to be valid moves. At each time step, the agent moves to one of these allowed cells with equal probability, and updates its orientation accordingly. There are therefore 255 total possible walk strategies of this type, excluding the condition of no movement whatsoever. A formal mathematical description of this class of random walks is presented in the Appendix. Many spatial models with mobile agents have used random walks of this type (e.g. Bonabeau, 1997; Epstein, 1998, 2002; Pepper and Smuts, 2002; Aktipis, 2004; Panait and Luke, 2004; Beltran et al., 2006; Vainstein et al., 2007; Nonaka and Holme, 2007; de Andrade et al., 2009), but few studies have compared multiple movement strategies (cf. Meloni et al., 2009; Smaldino and Schank, 2012).

To quantify each walk, we considered the average number of unique cells entered by a lone agent in  $t$  time steps; this metric is abbreviated  $UC_t$ . To clarify, we placed a single agent in a large space (length  $L > 2t$ ) and counted the number of distinct cells entered by the agent in  $t$  time steps. A deterministic walk

**Table 1**

Random walk strategies of interest, with brief descriptors, listed in order of decreasing exploratoriness.

	Brief descriptor	$UC_{100}$	Notes
	Speedster (SP)	98.51	The most exploratory random walk strategy. Also used in a recent ant foraging model (Panait and Luke, 2004).
	Zigzag (ZZ)	95.17	Many organisms move forward by alternating small movements to the forward-right and forward-left (Beer et al., 1997). This random walk strategy only slightly more restricted than Speedster.
	Forward-Left-Right (FLR)	73.65	An intermediately exploratory symmetrical random walk strategy between Zigzag and Brownian.
	Brownian (BR)	60.43	Pure random walk strategy for Moore neighborhood. Used in models of the evolution of cooperation (Pepper and Smuts, 2002).
	Sidestep (SS)	55.34	Used in Walkaway model of cooperation (Aktipis, 2004). Can also approximate the movement of 10-day-old rat pups in a rectangular arena (Schank, 2008).
	von Neumann (VN)	48.96	Pure random walk strategy for von Neumann neighborhood. Used in spatial prisoner's dilemma models (Epstein, 1998; Vainstein et al., 2007) and insect foraging (Bonabeau, 1997).
	Close-to-Home (CH)	34.85	Can approximate the movement of 7-day-old rat pups in a rectangular arena (Schank, 2008).
	Cyclone (CY)	30.69	The random walk strategy with the highest mean density, meaning that entered cells tended to be adjacent to many other entered cells.
	Tail Chaser (TC)	13.52	The most restricted random walk strategy.

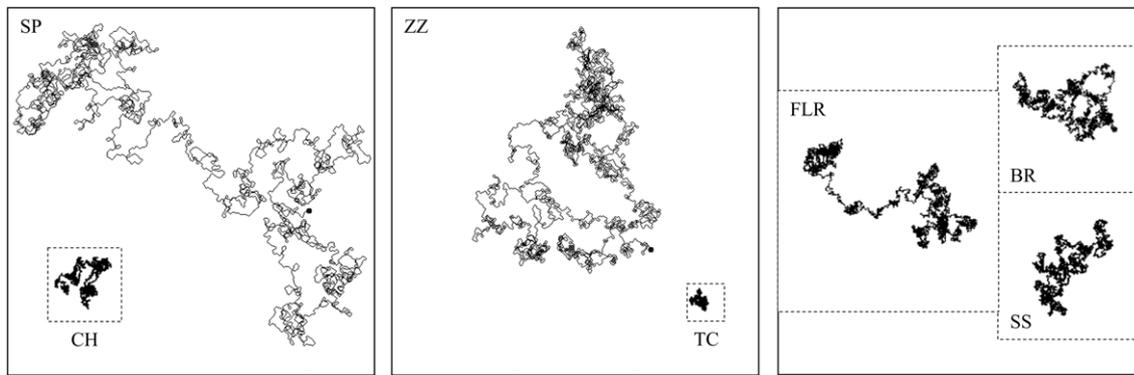
that always moved forward would have  $UC_t = t$ , while a walk that always moved backward would oscillate between two cells and thus have  $UC_t = 2$  for all  $t > 1$ . For our measurements, we averaged across 1000 runs for each random walk considered.

We tested every possible walk in our defined class, and settled on nine strategies that are of general interest and are representative of the range of possible random movement strategies (Table 1). For ease of discussion, we assigned each of these walks a brief descriptor and corresponding abbreviation.

In a finite space,  $UC_t/t$  will start at one and tend to zero as  $t \rightarrow \infty$  for all random walks, as the agent eventually enters every possible cell. Random walk strategies for which this quantity approaches zero slowly can be considered highly *exploratory*, as the agent tends to keep visiting new locations. Strategies for which  $UC_t/t$  falls rapidly, on the other hand, may be considered more *restricted*, as agents tend to revisit previously visited locations and maintain more consistent local neighborhoods. We ensured that our nine strategies of interest produced random walks that span the range between maximally exploratory and maximally restricted, based on the measure of  $UC_{100}$ , which was chosen

because simulation runs were usually on the order of a few hundred time steps. It is possible to associate exploratory behavior with other metrics, such as the average Euclidean distance traveled in  $t$  time steps,  $d(t)$ . The metric of unique cells was chosen because of its extremely high correlation with simulation outcomes, though correlation between  $UC_t$  and  $d(t)$  was predictably very strong.

It is possible that these random walks accurately describe the specific observed behaviors of biological organisms. For example, Close-to-Home and Sidestep can approximate the movement probability matrices of rat pups at seven and ten days old, respectively (Schank, 2008), and Zigzag may resemble the alternating left–right movement seen in many species (Beer et al., 1997). Speedster is a discrete simplification of correlated random walk, used to model movement in a variety of animals (Codling et al., 2008). More importantly, we view random walks as representing generic characteristics of how individuals move in space, at least in the tendency to either remain in a local area and repeatedly search or explore it, or to roam over a larger area, searching and exploring more broadly but less thoroughly. Individual movement may of course be either more exploratory



**Fig. 2.** Example path trajectories from random movement strategies (Table 1) at  $t = 10,000$ . The random walks are represented to scale in relation to the three large squares, each  $500 \times 500$  cells.

or more restricted than is captured by simple random walks through two-dimensional space. For example, humans have cars and planes and social media that allow them to interact with far more individuals than are present in their immediate vicinity. On the other hand, organisms may have their mobility options limited by the presence of physical obstacles or by the need to traverse certain paths. Nevertheless, quite a wide range of mobility is captured by the random movement strategies considered here.

For illustration purposes, Fig. 2 shows characteristic trajectory plots for some of the random movement strategies over 10,000 time steps. Highly exploratory strategies like Speedster and Zigzag cover much more territory than restricted strategies like Tail-Chaser or Close-to-Home.

## 2.2. Simulation outcomes

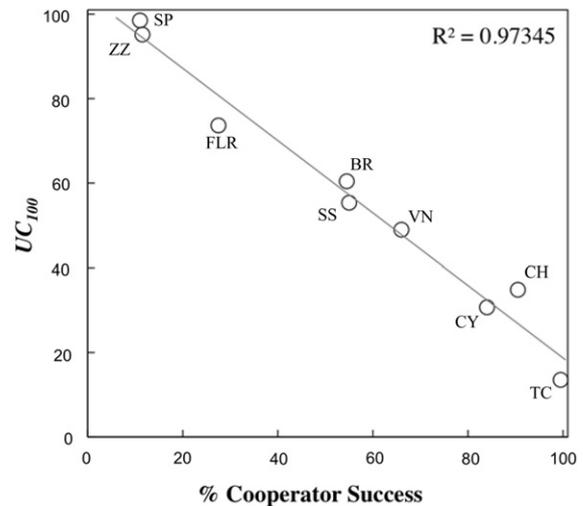
We ran 81 batches of simulations, assuming that cooperators and defectors could use different random movement strategies. For each batch, we performed 200 runs. We allowed simulations to run for a maximum of 200,000 time steps, though the vast majority finished in far less time—a simulation run ended when all the remaining agents were of the same type (cooperator or defector). Some runs in which defectors used the SP or ZZ movement strategies timed out with nonzero populations of both strategies (see discussion below). All other runs ended with one strategy completely disappearing, which we considered a victory for the other strategy, usually within 500 time steps. Any run that did not end in a defector victory was considered a “success” for cooperators.

## 3. Results

### 3.1. Basic model: limited dispersal and finite local capacity

We first considered simulation runs in which all agents used the same random movement strategy. Simulation outcomes were heavily influenced by the agents’ random movement strategy. The proportion of runs in which cooperators were successful is plotted against the  $UC_{100}$  of the random walk strategy used by the agents in Fig. 3. A linear regression on the data shows that the probability of cooperators succeeding against defectors was predicted almost entirely by agent movement strategy ( $R^2 = 0.97345$ ). If only runs in which cooperators were victorious were counted, the correlation increased slightly ( $R^2 = 0.97819$ ). Thus, random movement strategy predicted game outcomes very well.

While a nearly strictly linear relationship is surprising, the relationship is consistent with the previous theoretical analyses. When individuals used restricted random movement strategies, cooperators could form stable groups and outcompete defectors, who might initially exploit nearby cooperators but who had

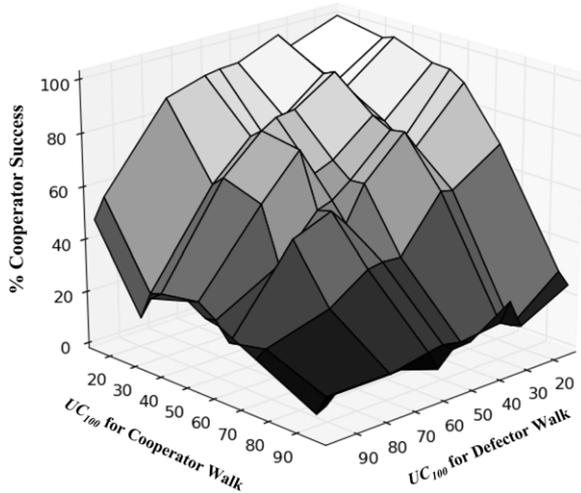


**Fig. 3.** Mean number of unique cells visited by a solitary agent at  $t = 100$  using each movement strategy plotted against the percentage of simulations won (or not lost by  $t = 200,000$ ) by cooperators when all agents employed the given movement strategy.

difficulty subsequently locating new cooperators following the deaths of their original victims. In contrast, when agents moved expediently through their environment (i.e., when they used more exploratory walks), defectors were able to easily find cooperators, and cooperative groups were much less stable as individuals often strayed far from their natal environments.

Next, we considered runs in which cooperator and defector movement strategies could differ, and found that the random movement strategies of both cooperators and defectors contributed to simulation outcomes. Cooperators did very well when agents used highly restricted random walks (Fig. 4). This, when combined with local reproduction, allowed coalitions of cooperators to stick together. When cooperators’ movement strategies were more exploratory, they were less likely to interact with other cooperators and more likely to run into defectors. Defectors likewise did well when they used exploratory random movement strategies. Unlike cooperators, defectors do best when they *negatively assort*, and exploratory movement tends to take them away from fellow defectors to where they are more likely to find new cooperators to exploit and can reproduce other defectors. Highly exploratory defectors limited (but did not eliminate) the chance of cooperator success, even when cooperator movement was highly restricted.

Existing theory predicts that exploratory movement should reduce cooperation (Houston, 1993; Vainstein et al., 2007; Meloni et al., 2009). However, highly exploratory movement did not always lead to a victory for defectors. Because defectors rarely



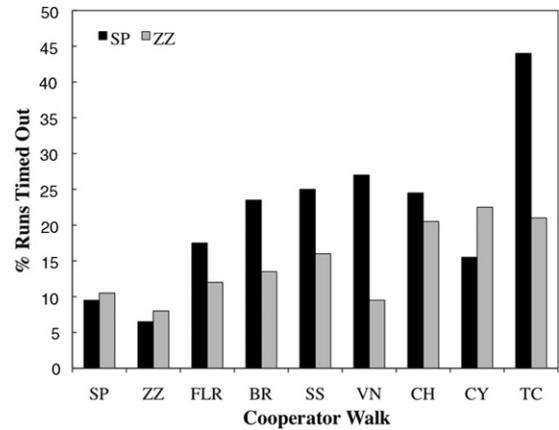
**Fig. 4.** Proportion of runs ending with cooperator success when cooperators and defectors use different random movement strategies. More restricted movement on the part of both types of agents contributed to more cooperator success. More exploratory random movement strategies tended to contribute to more defector success.

remained long in a given area, cooperators could form tight, stable clusters, sustained by mutual cooperation and local reproduction even though surrounded by fast moving defectors that limited cooperator growth (Fig. 5). This resulted in mixed populations that could persist indefinitely (we only tested to 200,000 time steps). These “time outs” occurred only when defectors used one of the two most highly exploratory movement strategies (Speedster or Zigzag), and tended to occur more often when cooperators used highly restricted walks, which facilitated cooperator clustering (Fig. 6). These results indicate that tendencies for more exploratory or restricted movement may have more profound and subtle effects in evolutionary dynamics than previously supposed.

The phenomenon of sustained mixed populations was driven by the emergence and maintenance of demographic zones of cooperation (Epstein, 1998), with newly born agents inheriting the environments of their progenitors (via local reproduction), a process known as *environmental* (Goodnight et al., 2008) or *ecological inheritance* (Odling-Smee et al., 2003). The ability to form these demographic zones is dependent on the restriction of one agent per cell, which translates to a local space capacity. As we will show, relaxation of this assumption can dramatically influence population dynamics.

### 3.2. Assumptions concerning local space capacity and limited dispersal

Our basic model makes two crucial assumptions about the world in which agents moved, interacted, and reproduced. First,



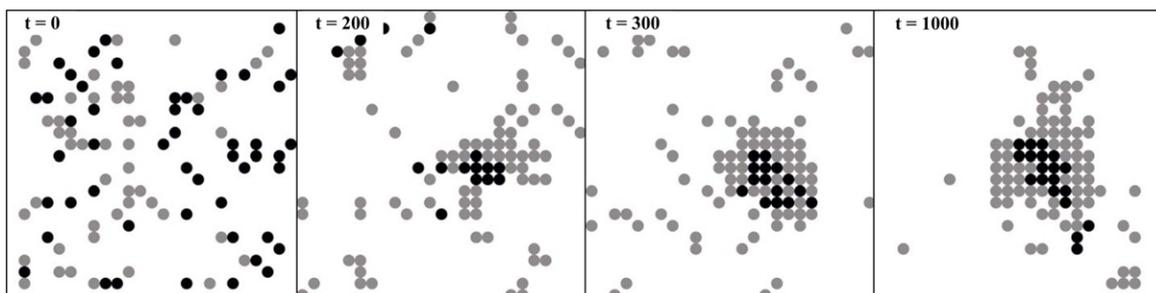
**Fig. 6.** Proportion of runs that timed out after 200,000 time steps when defectors used the SP or ZZ walks under limited dispersal and finite local capacity.

local space capacity is a local limitation on growth and movement: occupying a location creates a physical presence that other agents cannot enter. Second, dispersal is limited: offspring are born close to their parents and are therefore likely to interact with them. While we have shown that random movement strategies influence cooperation under some conditions, it is important to assess the robustness of these findings.

Here, *finite local capacity* refers to the limitation of one agent per cell as described above, and *unlimited local capacity* refers to the omission of this constraint, in which agents were allowed to occupy the same cell and found co-players from among those individuals at the same location, as in Aktipis (2004). In both cases, the global carrying capacity remains unchanged. *Limited dispersal* refers to the reproduction of offspring in an adjacent cell as described above, while under *random dispersal* offspring are reproduced in a random location within the entire space. Dispersal still had to meet the restrictions of local capacity constraints, so offspring could not be placed in an already-occupied location under finite local capacity. We ran the same set of simulations described in 3.1. to test the influences of finite local capacity and limited dispersal.

#### 3.2.1. Finite local capacity and random dispersal

When agents were restricted to unique spatial locations but reproduced randomly, cooperators were unable to form lasting clusters or avoid exploitation by defectors for any combination of random movement strategies, and defectors were victorious in all cases. These conditions made it very difficult for cooperative clusters to persist regardless of movement strategy, highlighting the importance of limited dispersal for the evolution of cooperation. This is exactly what we should expect if the formation of relatively stable demographic zones are required for the persistence of cooperators in a population.



**Fig. 5.** Screen shots of a representative simulation that did not end in a victory for either defectors or cooperators. Cooperators (black) used TC, defectors (gray) used SP. Scenarios like this occurred only when defectors used the most exploratory walks, SP or ZZ.

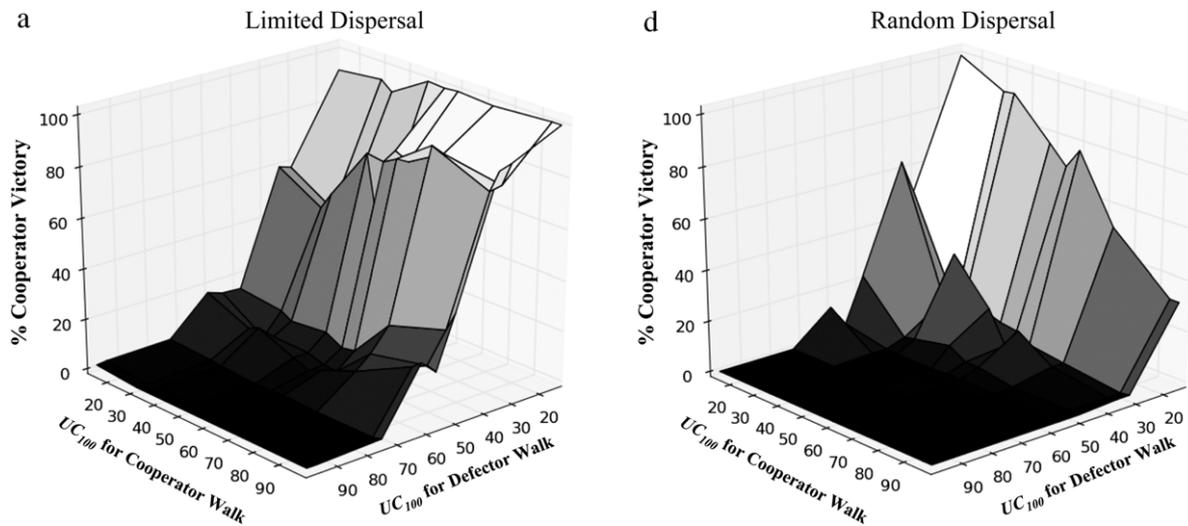


Fig. 7. Proportion of runs ending with a cooperator victory under unlimited local capacity. Results differed depending on whether dispersal was limited (A) or random (B).

### 3.2.2. Unlimited local capacity and limited dispersal

Without local capacity constraints, clusters of cooperators could not keep out defectors, so the success of cooperators was almost entirely dependent on defector movement. This was particularly true when dispersal was limited, because it allowed cooperators to spatially assort, and therefore the burden on defectors to find cooperators was amplified (Fig. 7(a)). When defectors used a highly exploratory walk, they covered space very effectively, and were not impeded by physical clusters of cooperators or even clouds of other defectors. Cooperators, on the other hand, could form very large groups in very little territory, and had less need to move to find co-players. Interestingly, when defectors used a restricted random movement strategy, cooperators using an exploratory walk did far better when local capacity was unlimited than when it was finite. The ability of multiple agents to co-occupy cells led to an increase in the amount of vacant space, and drastically decreased the chance of a randomly moving cooperator encountering restricted-movement defectors.

### 3.2.3. Unlimited local capacity and random dispersal

Under random dispersal, it was harder for cooperator clusters to remain localized, and defectors won over a greater range of movement strategies than when dispersal was limited. As in Section 3.2.2, cooperators did not persist against defectors using exploratory random movement strategies, and this effect was amplified by random dispersal (Fig. 7(b)). Cooperators again did better against restricted-movement defectors by restricting their own movement. Since the locations of defectors were no longer correlated with one another, cooperators did best by avoiding far-ranging spatial exploration.

## 3.3. Interaction dynamics

We collected data on the number of total and unique interactions agent had over the course of their lives. The *interaction rate* is the proportion of times steps over an agent's lifespan in which the agent played the PD game rather than attempt movement (Fig. 8). The number of *unique interactions* is the number of unique game partners an agent had over its lifespan (Fig. 9). These metrics allowed us to directly relate the simulation outcomes to measures of how frequently agents needed to look for new partners (the interaction rate) and how varied individual social networks were (unique interactions). They also allow us to begin to build a bridge between spatial models with mobile agents

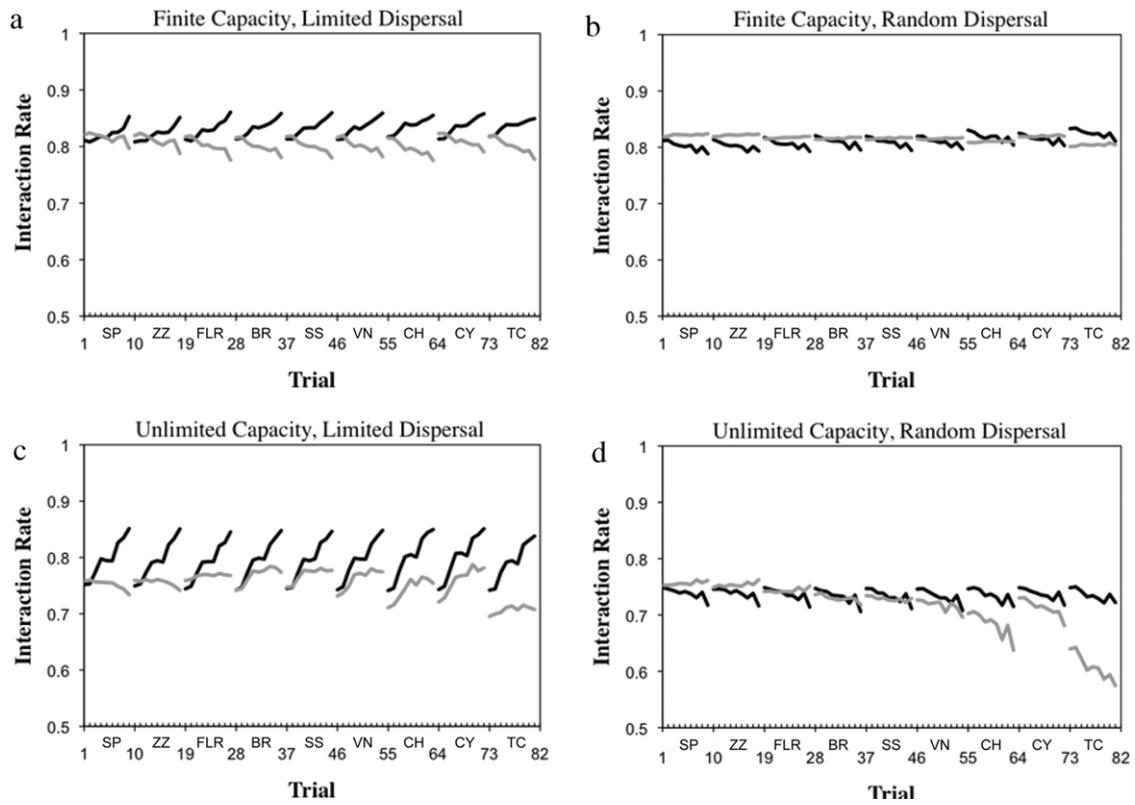
and studies of games on dynamic networks (e.g. Pacheco et al., 2006; Santos et al., 2006; Perc and Szolnoki, 2010; Van Segbroeck et al., 2010).

Under finite local capacity and limited dispersal, cooperators' interaction rates increased as they used more restricted movement strategies, while defectors' interaction rates decreased. This divide widened when defectors used more restricted movement strategies. As both cooperators and defectors used more restricted movement strategies, the number unique interactions decreased for defectors but tended to increase for cooperators. This fits well with the finding that cooperators did best when all agents used restricted movement strategies; restricted movement allow cooperators to interact more with each other and less with defectors.

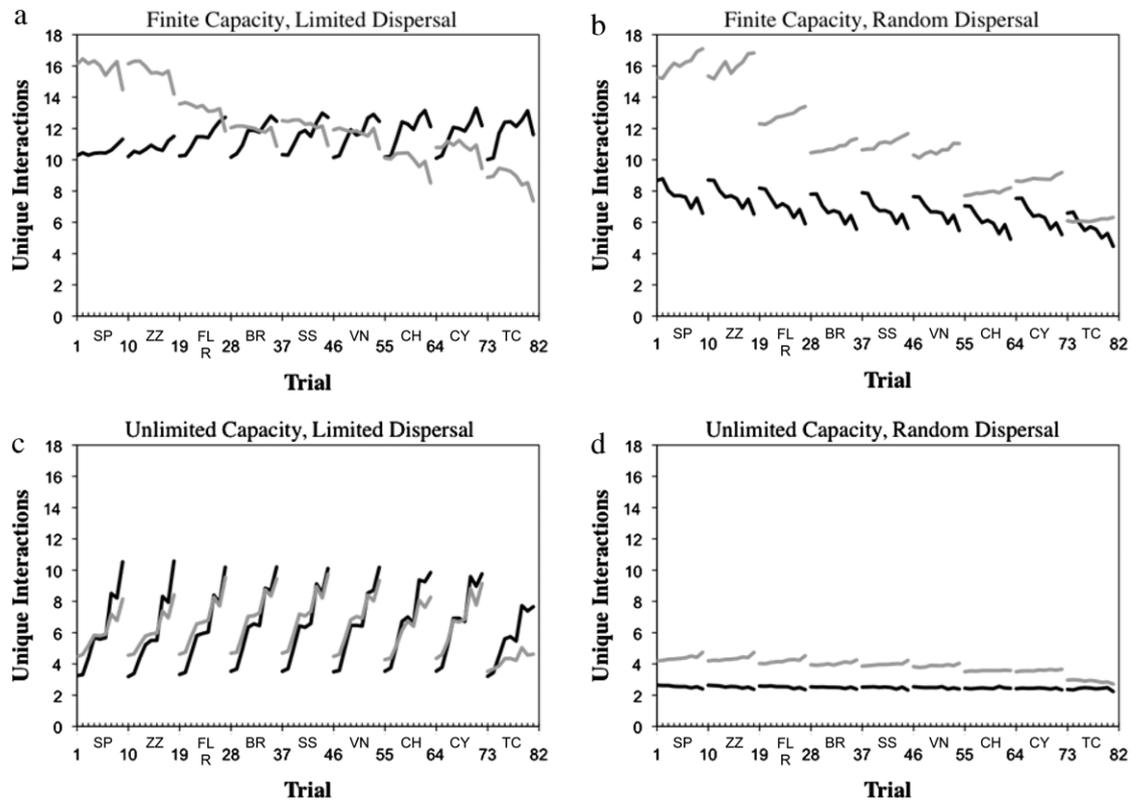
Defectors always won when local capacity was finite and dispersal was limited, and interaction rates were not overly sensitive to agents' movement strategies. Movement strategies still influenced the interaction statistics, however. Cooperators had lower interaction rates and fewer unique interactions when they used more restricted movement strategies. Defectors also had fewer unique interactions as they used more restricted walks. These results highlight the fact that cooperator success relies not principally on the number of interactions, but on the amount of positive assortment—the extent to which cooperators can preferentially interact with cooperators and avoid defectors. Finite local capacity and random dispersal prevented cooperators from forming cohesive spatial clusters, and made them easy prey for exploitative defectors.

Under limited dispersal and unlimited local capacity, the probability of a cooperator victory was almost entirely dependent on defectors' movement strategy, but the interaction rates and the number of unique interactions were almost entirely dependent on cooperators' movement strategy; agents had more interactions when cooperators used more restricted walks. However, defectors' interaction rates also increased, if slightly, when they used more exploratory movement strategies. Although this effect is relatively small (Fig. 8(c)), the inability of cooperator clusters to keep out defectors meant that even small increases to defectors' interaction rates facilitated their victory over cooperators.

Finally, when local capacity was unlimited and dispersal was random, game outcomes were largely dependent on defector movement strategies, but cooperators also did better when they used more restricted walks. In these scenarios, individual locations could host indefinitely many agents and random dispersal eliminated the spatial correlation between parents and offspring. As



**Fig. 8.** The average interaction rate for cooperators (black) and defectors (grey) for all simulation conditions. An agent's interaction rate is the proportion of time steps in the agent's life in which a game interaction occurred. For each capacity/dispersal condition, 81 trials occurred in nine blocks of nine trials, with each trial consisting of 200 runs. Blocks were run in order of increasingly restricted defector movement strategies (indicated by the movement strategies' abbreviations). Within each block all nine cooperator movement strategies were tested, in the same order of increasing restrictedness.



**Fig. 9.** The average number of unique interactions for cooperators (black) and defectors (grey) for all simulation conditions. The number of unique interactions for an agent is the number of unique individuals with whom the agent played the PD game throughout the agent's lifespan. For each capacity/dispersal condition, 81 trials occurred in nine blocks of nine trials, with each trial consisting of 200 runs. Blocks were run in order of increasingly restricted defector movement strategies (indicated by the movement strategies' abbreviations). Within each block all nine cooperator movement strategies were tested, in the same order of increasing restrictedness.

such, agents in this condition had the lowest number of unique interactions among the four capacity/dispersal conditions. Cooperators' interaction rates were slightly lower when their own movement strategies were more restricted, and defectors' interaction rates were lower when both their own and cooperators' movement strategies were more restricted. Interestingly, defectors' unique interactions were influenced by an interaction between defector and cooperator movement strategies (Fig. 9(d)). When defectors used highly exploratory movement strategies, their unique interactions increased when cooperator movement was more restricted, as exploratory defectors could find groups of cooperators better when the cooperators tended to remain confined to small spatial areas. However, this effect diminished when defector movement was more restricted, and was reversed when defectors used the most restricted walk, Tail-Chaser. In this case, restricted-movement defectors required highly mobile cooperators to find them. This explains why, in this condition, cooperators did best when all agents used restricted movement strategies.

#### 4. Discussion

We have provided the first detailed analysis of different random movement strategies on the evolution of cooperation for varying conditions of dispersal and local neighborhood size. Strategies of random movement used by altruistic and selfish individuals alter cooperators' chances of success, and those effects interact with both dispersal and local space capacities. These results generally confirm previous studies which considered mobility, neighborhood size, or dispersal individually (Houston, 1993; Koella, 2000; Mitteldorf and Wilson, 2000; Aktipis, 2004; Pepper, 2007; Számadó et al., 2008; Lion and van Baalen, 2008; Helbing and Yu, 2009; Meloni et al., 2009; Smaldino and Lubell, 2011), but also show that these effects may be more nuanced than previously considered. Under constraints of dispersal and local neighborhood size, the degree to which a random movement strategy is exploratory not only influenced population dynamics, but did so in a systematic way. Cooperators had the most success when individuals used restricted random movement strategies and defectors did best when individuals used exploratory random movement strategies, but exploratory movement on the part of defectors allowed spatial clusters of cooperators, if formed, to persist indefinitely in mixed populations.

These results, however, were highly dependent on the assumptions of dispersal and neighborhood size and the effects were not additive. In the absence of limited dispersal, finite local capacities caused agents to be spread more widely throughout the environment, which made it impossible for cooperators to successfully dominate, regardless of agent movement strategy. Additionally, while highly exploratory defector movement tended to limit cooperation, it also produced stable mixed equilibria under conditions of limited dispersal and finite local capacities, particularly when cooperator movement was restricted.

In all conditions of dispersal and local capacity where cooperators were able to succeed, we note that the probability of cooperator success did not have a strictly monotonic relationship with  $UC_{100}$  – i.e., cooperator success did not always increase with decreased  $UC_{100}$ , as in Fig. 4 – which means that this metric does not completely explain the results. This is unsurprising, because the number of unique cells entered does not fully describe the random walks. What is noteworthy is the extent to which it *does* explain the results, which indicates that  $UC_t$  is a good metric for the exploratory nature of a random walk in a discrete space. Other factors, however, were also operating. For example, with finite local capacities and limited dispersal, mobility not only influenced the likelihood of finding a game partner, but also access to empty patches necessary for reproduction. However, since proximity to

other agents was necessary to receive positive payoffs, this effect is likely to have been very small compared with the importance of locating cooperators and avoiding defectors.

##### 4.1. Invasion

All the simulations in the preceding sections began with equal numbers of cooperators and defectors (which also meant equal numbers of agents using the two corresponding random movement strategies). While it is a common technique in spatial evolutionary games to begin simulations with equal numbers of phenotypes, this methodology also limits our ability to assess invasion dynamics. It is unclear, however, how to perform something equivalent to an ESS analysis in an agent-based system such as the one presented here. If, for example, small numbers of cooperators are introduced in random locations, it is well known that they can almost never invade because they are isolated, whereas the same small number of cooperators introduced in a spatial cluster is much more likely to succeed, as indicated by our unpublished results. A careful study of invasion dynamics in spatially organized populations would be an interesting approach for future research. The work presented here aimed to explore the consequences of different random movement strategies under well-understood conditions in order to determine those patterns of movement contribute to the evolution of cooperation.

##### 4.2. Grid size and population density

The values for grid size and population density in our model have been used in previous work on mobility and cooperation (Aktipis, 2004, 2006). To ensure that our results were not dependent on the size of the spatial grid, we ran simulations using a  $50 \times 50$  grid and a global population of 400 agents to keep the density constant. For all conditions under random dispersal and for limited dispersal and unlimited local capacity, the results were qualitatively identical to the runs using a  $25 \times 25$  grid. Under limited dispersal and finite local capacity, the increased number of empty cells increased the ability of cooperators to initially assort and form spatial clusters. This had the effect of increasing the number of cooperator victories across the board, as well as the number of runs that timed out with stable two-strategy equilibria when defectors used the three most exploratory random movement strategies. Thus, the tight linear correlation shown in Fig. 3 was dependent on the grid size used. However, the qualitative results still held: cooperators had more victories when all agents used restricted movement, and stable mixed equilibria could occur when cooperators assorted and defectors used highly exploratory random movement strategies.

Differences between movement strategies likely matter less in very dense environments, since individuals will encounter each other quickly regardless of movement strategy. There are many other possible environmental assumptions in addition to those considered here. Our results do not necessarily hold for all possible environments; what we have shown is that under general and previously considered assumptions, the specific characteristics of random movement strategies used by agents influence social interactions and long-term evolutionary dynamics.

##### 4.3. Movement strategies matter in models of social evolution

The ways individuals move in space affect the variety and extent of their social interactions. Our results show that mobility may have had an important role in the evolution of cooperation. Movement strategies and patterns may be no less important in the evolution of cooperation than cognitive strategies. Thus, we believe that developing theories of mobility is essential for applying game theoretic models to animal and human cooperative

contexts. The random movement strategies we analyzed all had the same probability of movement in each round and the same step size; they varied only in their degree of exploration of the environment. Just as different random walks – independent of step length – can influence foraging success (Bartumeus et al., 2005; Hills, 2006), differences in exploratory behavior (resulting from different random movement strategies) can influence processes of social evolution.

The different random movement strategies could be viewed as generic representations of characteristics of individual movement behavior. For example, a specific random movement strategy may represent the tendency for novelty seeking by producing more exploratory walks, or another random movement strategy may represent the tendency for staying close to where resources have been previously found, thus producing more restricted random walks. An interesting possibility not considered in our simulations is for a single individual to possess a repertoire of multiple random walks, used contingently based on experience and the need for exploratory or restricted movement.

For more abstract social models, different random movement strategies could represent differences in “social mobility”, influencing the rates at which individuals encounter new partners (Smaldino and Schank, 2012). In this context, an individual’s local neighborhood becomes a *de facto* dynamic social network. We examined some simple measures of agent interaction dynamics and found that they provided additional explanatory insight into the success or failure of cooperators in some but not all cases. An interesting direction for future research would be to use more sophisticated approaches from social network theory (Carley, 2003; Scott and Carrington, 2011) in a model of this type to investigate the influence of spatial and mobility constraints on network properties of agent populations. Here, we have shown that the choice of random movement strategy is not trivial in modeling behavior. Our results support investigating multiple random movement strategies in agent-based models of social behavior and require future research that integrates cognitive, spatial, and mobility approaches in the study of social evolution.

## Acknowledgments

We thank Shane Celis, James Crutchfield, Richard McElreath, Matt Miller, Kevin Ringelman, and two anonymous reviewers for helpful comments. We also thank NIH (1R21HD061716-01A1) for funding support.

## Appendix. Numbering scheme for discrete, oriented random walks

In this paper, we considered nine random walk strategies, chosen for theoretical relevance and to cover a wide range of results on the metric  $UC_t$ . We gave each walk a brief descriptor in order to facilitate discussion. Another potential means of classification would be to assign a number to each random walk strategy. Because movement in this class of random walks is constrained to eight neighboring cells such that movement to each is either allowed or prohibited, we propose a general numbering system, inspired by Wolfram’s (2002) numbering scheme for classifying one-dimensional binary cellular automata. This will allow future work to easily refer to any particular random walk strategy of this class by a single number between 0 and 255, rather than requiring a diagram for each walk.

Let the cell directly in front of an agent be numbered zero, the cell to the agent’s forward-right be numbered one, and so on

clockwise up to seven at the agent’s forward-left. A movement strategy  $a$  is numbered

$$a = \sum_{i=0}^7 \delta_i 2^i, \quad (1)$$

where  $\delta_i$  is equal to 1 if the cell referenced by the subscript is an allowed move, and zero otherwise. For example, the “Zigzag” walk, which always moves to the forward-right or forward-left, has the number 130 ( $2^1 + 2^7$ ).

In the work presented in this paper, we ignored differences between left- and right-based random movement strategies. Accordingly, if a random movement strategy was not laterally symmetrical (i.e., Tail-Chaser and Cyclone), we arbitrarily used only the right-biased version. Over the range of all possible random movement strategies in our class, we can easily determine the reference number of a laterally asymmetric movement strategy’s “mirror image”. A strategy’s lateral reflection,  $a^*$ , has the number

$$a^* = \delta_0 + 2^8 \cdot \sum_{i=1}^7 \delta_i 2^{-i}. \quad (2)$$

We then define two strategies  $a$  and  $b$  as *mirror equivalent* if and only if  $b = a^*$ .

There are nine movement strategies in this class that are uninteresting for agents in a two-dimensional space. These are the eight deterministic movement strategies  $2^i$ , and #17, which always moves either forward or backward, and generates a one-dimensional Brownian walk (Berg, 1993). We are then left with 246 random movement strategies, which drops to 137 if we also eliminate one from every pair of mirror equivalent strategies.

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