

# Spatial evolutionary dynamics produce a negative cooperation–population size relationship

Edward W. Tekwa<sup>a,b,\*</sup>, Andrew Gonzalez<sup>b</sup>, Michel Loreau<sup>c</sup>

<sup>a</sup> Department of Ecology, Evolution, and Natural Resources, Rutgers University, 14 College Farm Road, New Brunswick, NJ, 08901, USA

<sup>b</sup> Department of Biology, McGill University, 1205 Dr. Penfield, Montreal, QC, H3A 1B1, Canada

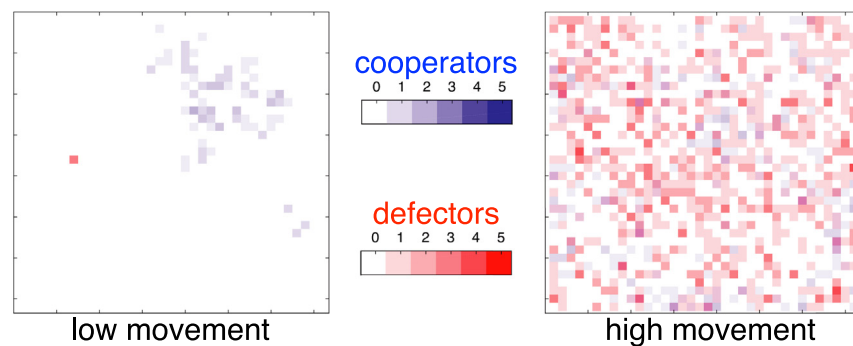
<sup>c</sup> Theoretical and Experimental Ecology Station, CNRS and Paul Sabatier University, 09200, Moulis, France



## HIGHLIGHTS

- Cooperation only increases population size when it is sufficiently beneficial.
- Spatial clustering creates a negative cooperation–population size relationship.
- Cooperation faces the ecological dilemma of small population even when selected for.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Natural selection can favour cooperation, but it is unclear when cooperative populations should be larger than less cooperative ones. While experiments have shown that cooperation can increase population size, cooperation and population size can become negatively correlated if spatial processes affect both variables in opposite directions. We use a simple mathematical model of spatial common-pool resource production to investigate how space affects the cooperation–population size relationship. We find that only cooperation that is sufficiently beneficial to neighbours increases population size. However, spatial clustering variations can create a negative cooperation–population relationship between populations even when cooperation is highly beneficial, because clustering selects for cooperation but decreases population size. Individual-based simulations with variable individual movement rates produced variation in spatial clustering and the hypothesized negative cooperation–population relationships. These results suggest that variation in spatial clustering can limit the size of evolutionarily stable cooperating populations – an ecological dilemma of cooperation.

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## 1. Introduction

How cooperation evolves is an important question of general interest to evolutionary biologists, ecologists, biomedical researchers

\* Corresponding author at: Department of Ecology, Evolution, and Natural Resources, Rutgers University, 14 College Farm Road, New Brunswick, NJ, 08901, USA.

E-mail address: [wongtekwa@gmail.com](mailto:wongtekwa@gmail.com) (E.W. Tekwa).

and human demographers (Hamilton, 1975). Cooperation in animals (Wilson, 1975), pathogens (Buckling et al., 2007), and humans (Hardin, 1968) is not only behaviourally interesting, it can also strongly affect demographic dynamics and thus ecological outcomes (Schoener, 2011; Wakano et al., 2009). At the extremes, evolution by natural selection can drive populations to either collapse (Webb, 2003) or be rescued (Bell and Gonzalez, 2011). However, the theoretical relationship between cooperation and population size (cooperation–population relationship, for short) has

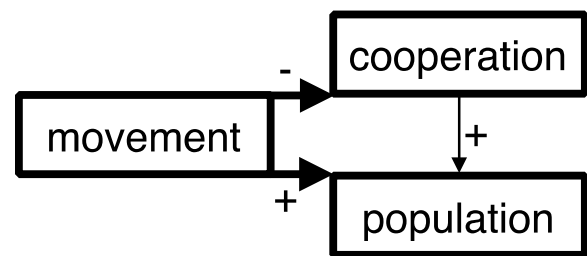
not been formally explored, even though a positive relationship is often implicitly assumed.

Early on, natural selection was often assumed to act on entire populations, leading individuals to cooperate (Kropotkin, 1902; Wynne-Edwards, 1963). Hamilton's cooperation theory questioned the concept of population adaptation and refocused natural selection on the individual level (Hamilton, 1964). While it is now accepted that cooperative behaviours can evolve through selection at a higher level than that of the individual (Keller, 1999; Okasha, 2006), it remains unclear whether such selection should generally increase overall population size, since cooperation is often modelled without explicit demographic dynamics. A growing body of literature addresses spatial, evolutionary, and demographic dynamics in conjunction (van Baalen and Rand, 1998; Epstein, 1998; Koella, 2000; Pfeiffer et al., 2001; Rousset and Ronce, 2004; Wakano et al., 2009; Lion and Gandon, 2010; Smaldino et al., 2013), but how spatial cooperation affects population size has not been formally analysed. Conceptually, several theories, including public-good (Hauert et al., 2006), common-pool resource (Levin, 2014), and cooperation creating population elasticity (Van Dyken and Wade, 2012), encapsulate the expectation that cooperation benefits the population. Indeed, a positive relationship between cooperation and population size has been consistently observed in experiments (Velicer, 2003; Chuang et al., 2009; Smith et al., 2010; Tekwa et al., 2017).

However, some theorists have speculated that the cooperation–population relationship is not necessarily positive. Darwin remarked: “actions are regarded as good or bad, solely as they obviously affect the welfare of the tribe – not that of the species” (Darwin, 1871), suggesting a multilevel selection view that natural selection for cooperation acts at some intermediary level above individuals, and that the effect of cooperation on the population is invisible to selection. Hamilton took a stronger position regarding the conflict between groups and populations. He wrote about cheating or selfishness that, “when suppressed at one level, (it) gathers its strength at another” (Hamilton, 1975), implying that local cooperation can often harm the global population. A number of recent models incidentally showed that top-down population limits (Ohtsuki et al., 2006; Taylor et al., 2007) and growth-induced pattern formation (Wakano et al., 2009; Smaldino et al., 2013) can create a negative relationship between cooperation and population size, but these works focused on evolutionary dynamics and did not explicitly discuss the cooperation–population relationship. It is thus unknown what causes cooperative populations to be large or small relative to less cooperative populations.

We hypothesize that spatial clustering is a bottom-up factor that affects both cooperation and population size and can determine their relationship. Spatial clustering is a salient feature of many cooperative phenomena. Cooperation in bacteria (Buckling et al., 2007; Tekwa et al., 2015b), the evolution of multicellularity (Michod and Roze, 2001), ant colony formation (Wilson, 1975), and bird cooperative breeding (Cornwallis et al., 2017) have limited spatial ranges that do not directly affect entire populations and thus are local, not global, public goods or common-pool resource interactions. This kind of locally selected cooperation should increase local densities but does not guarantee elevated population size. This leaves the possibility that spatial clustering can affect cooperation and population size in opposite directions.

Movement rate is an important source of spatial clustering variation that can affect both cooperation and population size (Fig. 1). According to metapopulation (Hanski, 1991) and dispersal (Hamilton and May, 1977) theories increased movement rate should increase population size by alleviating local competition and maintaining the colonization of empty patches, but it should also decrease cooperation by exposing cooperators to defectors (Hamilton, 1964; Nowak et al., 1994; Koella, 2000; Taylor et al.,



**Fig. 1. Model causal pathways.** Movement rate decreases cooperator frequency and increases population density. Cooperation increases population density, and this effect is strengthened by movement rate.

2007; Lion and van Baalen, 2008; Tarnita et al., 2009; Smaldino and Schank, 2012; Perc et al., 2013; Débarre et al., 2014). Based on these well-established ecological and evolutionary principles, we propose that variation in spatial clustering could generate a negative statistical correlation between cooperation and population size despite a causally positive effect of cooperation on population size (Fig. 1), and this trend can be common within taxonomic groups that share similar non-spatial life histories but different spatial characteristics. Even though this negative relationship would be statistical rather than causal, the importance and ubiquity of spatial processes means that cooperation, even when it evolves, may also have to overcome an inherent tendency to be ecologically uncommon. We formalize our hypothesis by constructing a common-pool resource model and deriving analytical conditions for when the cooperation–population relationship should be negative. We check our model predictions using individual-based simulations and spatial metrics. We conclude by discussing the theory's implications for multilevel selection.

## 2. Theory

We construct a generic spatial common-pool resource model (Tekwa et al., 2017) involving asexual cooperator and defector cells. This model is similar to a traditional public-goods game, except that individuals also directly compete (are rivals) for an underlying resource that is produced cooperatively (Dionisio and Gordo, 2006). Our model relies on four main assumptions. First, cooperation is obligate and costly, which reduces the cooperator's intrinsic growth rate. Second, competition occurs between all individuals within a neighbourhood (or patch) and results in a finite population size. Third, cooperation alleviates competition within patch and can bestow a net benefit to neighbours at low local densities through an Allee effect (Courchamp et al., 1999). Fourth, mean spatial clustering metrics completely capture the positive assortments and segregation between cooperators and defectors.

### 2.1. Model setup

We first introduce the parameters of our model that describes the change in the global densities (numbers per area) of cooperators ( $X_c$ ) and defectors ( $X_d$ ).

The spatial parameters  $C_{ij}$  are continuous-space clustering coefficients that measure how many times more likely that an individual of one morph ( $i$ ) encounters another morph ( $j$ ) than under the well-mixed limit. Clustering, like related metrics such as relatedness, is an emergent property of birth, death, and movement (van Baalen and Rand, 1998; Bolker and Pacala, 1999), but in our mathematical analysis we first treat it as a set of parameters and ignore feedbacks from demography in order to isolate spatial effects. Note  $C_{ij}$  is different from clustering coefficient in network theory, but for short we will reference  $C_{ij}$  as clustering coefficient

from here on. Mean local densities are  $X_{ij} = C_{ij}X_j$ , which are the mean number of  $j$ -morph neighbours per area for the  $i$ -morph. Since  $X_iX_{ij}$  is the total density of  $ij$  pairs, and this density is the same when the indices  $i$  and  $j$  are switched,  $X_cC_{cd}X_d = X_dC_{dc}X_c$ , so  $C_{cd} = C_{dc}$  (Tekwa et al., 2015a). Clustering coefficients (or local densities) can be thought of as alternative decompositions of spatial elements to relatedness when interactions are indiscriminate, and their mathematical relationships have been previously established (Lion and Gandon, 2010; Tekwa et al., 2017). In later analyses, we will refer to two relatedness metrics:  $R_c$ , the relatedness between cooperators, and  $R_d$ , the relatedness between defectors, which can be written in terms of clustering coefficients (Supplementary Material Appendix: Related Spatial Metrics).

Defectors grow at an intrinsic rate of  $r$ , and cooperators at an intrinsic rate  $r-c$ , where  $c$  is the density-independent cost of cooperation. An individual receives, on average, a benefit  $a$  from neighbouring cooperators (which are mean local densities  $C_{cc}X_c$  for a focal cooperator, and  $C_{dc}X_c$  for a focal defector) (Matsuda et al., 1992; van Baalen and Rand, 1998; Lion and van Baalen, 2008; Tekwa et al., 2015a) and additionally experiences a cost of competition  $k$  from all neighbours ( $C_{ic}X_c + C_{id}X_d$ ) due to resource consumption. In a non-spatial game theoretic terminology, this indiscriminate competition subtracts  $k$  from all payoff entries and thus has no evolutionary effect (Nowak, 2006). Within-morph competition ( $kC_{ii}X_i$ ) can also be understood as kin competition (Wilson et al., 1992; Taylor, 1992), which does not necessarily impede the evolution of cooperation (Koella, 2000; Van Dyken and Wade, 2012; Tekwa et al., 2017). We assume that the cooperative and competitive effects are linearly additive, and that  $k > a$ , which follows the standard ecological principle that populations are self-limiting. This assumption does not force a negative cooperation–population relationship trivially, as it allows strong cooperation (population size reaches infinity due to cooperation when  $a \rightarrow k$ ), capturing the intuition that cooperation benefits the greater good. The dynamic system is written as:

$$\begin{aligned} \frac{dX_c}{dt} &= X_c (r - c + aC_{cc}X_c - k(C_{cc}X_c + C_{cd}X_d)) \\ \frac{dX_d}{dt} &= X_d (r + aC_{dc}X_c - k(C_{dc}X_c + C_{dd}X_d)) \end{aligned} \tag{1}$$

Introducing a net positive effect of cooperators at low local densities (Allee effect) to the model (Courchamp et al., 1999) would only add multiplicative terms to growth rates in Eq. (1) (SM Appendix: Model Generalization). Therefore, so long as cooperation is not essential for survival, we obtain the following equilibrium cooperator and defector densities regardless of whether cooperation only alleviates competition or bestows a net benefit (SM Appendix: Equilibria):

$$\begin{aligned} X_c &= \frac{(r - c) C_{dd} - rC_{cd}}{(k - a)(C_{cc}C_{dd} - C_{cd}^2)} \\ X_d &= \frac{rC_{cc} - (r - c)C_{cd}}{k(C_{cc}C_{dd} - C_{cd}^2)} \end{aligned} \tag{2}$$

2.2. Non-spatial condition for cooperation to increase population size

In monomorphic populations with only cooperators or only defectors (labelled with hat), equilibrium densities or carrying capacities without evolutionary interactions between morphs are  $\hat{X}_c = (r - c)/((k - a)\hat{C}_{cc})$  and  $\hat{X}_d = r/(k\hat{C}_{dd})$  for cooperators and defectors, respectively. These are obtained from Eq. (2) with  $C_{cd} = 0$  (the morphs do not meet in space). For cooperation to causally increase population size compared to defection,  $\hat{X}_c > \hat{X}_d$  in monomorphic populations. In the case where cooperator and defector clustering are either absent (all  $C = 1$ ) or identical

( $\hat{C}_{cc} = \hat{C}_{dd}$ ), the condition becomes (SM Appendix: Demographic Conditions):

$$c/a < r/k \tag{3}$$

Thus, in the absence of natural selection and clustering differences, cooperation does not increase the population size when cooperation is costly (high  $c/a$ ) relative to the size of a population without cooperation ( $r/k$ ). This condition is separate from the evolutionary condition for cooperation; as we will see in Section 2.4, cooperation can evolve even when it does not increase population size.

2.3. Effect of non-spatial variations

We now incorporate evolutionary dynamics and consider the effect of non-spatial parameter variations on the cooperation–population relationship. Analytical derivations based on partial derivatives (SM Appendix: Non-Spatial Parameters) reveal that the independent variations in each non-spatial life history parameter ( $k, r, c, a$ ) affect population size  $X (= X_c + X_d)$  and cooperator frequency  $P (= X_c/X)$  in the same direction and thus maintain a positive cooperator frequency–population size relationship across populations. The results are intuitive: an increase in either intrinsic growth rate ( $r$ ) or cooperation benefit ( $a$ ) enhances both cooperators and the whole population, while an increase in competition ( $k$ ) or cost of cooperation ( $c$ ) harms both cooperators and the population.

2.4. Effect of spatial variations

The full condition for cooperation to increase the populations size (from Eq. (2)) is (SM Appendix: Demographic Conditions):

$$k(r - c) > r(k - a)\hat{C}_{cc}/\hat{C}_{dd} \tag{4}$$

This condition becomes hard to attain if cooperator populations tend to be associated with higher clustering than defector populations through evolution ( $\hat{C}_{cc} > \hat{C}_{dd}$ ). Consider how this spatial condition can be attained. A common simplification of spatial dynamics in a mixed population is that in a saturated habitat (without demographic dynamics),  $C_{cc} = C_{dd} = C_{ii}$  (Nathanson et al., 2009; Débarre et al., 2014), and that this within-morph clustering increases with reduced movement rate (Matsuda et al., 1992; Bolker and Pacala, 1999). For cooperation to be selected for and likely fixed in the long term, a condition is  $X_c > X_d$ , which simplifies to (SM Appendix: Evolutionary Condition):

$$\frac{C_{ii}}{C_{cd}} - 1 > \frac{2k - a}{|ra/c - k|} \tag{5}$$

Thus, regardless of whether the non-spatial parameters dictate that a cooperative population in isolation should be greater ( $c/a < r/k$ ) or smaller ( $c/a > r/k$ ) than a defective population (terms in the denominator of the right hand side in Eq. (5)), cooperators can be evolutionarily favoured when clustering ( $C_{ii}/C_{cd}$ ) is sufficiently high. In particular, let  $C_{ii} = \hat{C}_{cc}$  be the within-morph clustering that favours cooperators, and let  $C_{ii} = \hat{C}_{dd}$  be the condition that favours defectors. Then, holding everything else constant,  $\hat{C}_{cc} > \hat{C}_{dd}$ , which is congruent with most theoretical conclusions (Nathanson et al., 2009; Tarnita et al., 2009; Tekwa et al., 2017). This result, in conjunction with Eq. (4), shows that spatial variation in density can create a negative relationship through evolution, even under conditions where cooperation should causally benefit both neighbours and the population.

In summary, high spatial clustering elevates competition for all, but favours cooperation because cooperators experience a lower per-neighbour competition. The elevated competition, coupled with selection at the expense of the intrinsic growth rate, means

that cooperative populations are often small. On the other hand, low spatial clustering releases individuals from competition, thus selection acts more directly on the intrinsic growth rate, which favours defectors and increases population size.

### 3. Simulation study

In general, spatial effects on cooperator frequency and population size cannot be easily obtained analytically when we consider the coupled dynamics of cooperation, population, and space (Tekwa et al., 2017). In particular, clustering coefficients, or their related metrics of relatedness, which we have treated so far as parameters, are in reality emergent properties of growth and movement. We therefore use individual-based simulations of Eq. (1) with varied movement rates to generate the spatial clustering conditions under which our theory above predicts a negative cooperation–population relationship. Movement rate is widely expected to decrease within-morph clustering (Matsuda et al., 1992; Bolker and Pacala, 1999). Thus, we expect that the cooperation–population relationship can be negative when movement rate varies across populations.

#### 3.1. Simulation setup

We use a  $36 \times 36$  patch landscape and randomly initialize the population in each patch with cooperators and defectors, each with independent Poisson rates of 0.1, meaning that each patch can start with any number of individuals, but global cooperator and defector densities start with means of 0.1. Over time, each patch can contain any number of individuals (Fig. 2a–c), which allows for a full range of demographic dynamics and avoids imposing the somewhat-artificial spatial competition in lattice or network setups where only one individual can occupy a patch (Lion and van Baalen, 2008; Van Dyken and Wade, 2012; Perc et al., 2013). The entire landscape can thus contain a much larger population than the number of patches suggests. Local population limitations arise endogenously from local interactions, which contrasts from other simulation setups where patches can contain multiple individuals, but global population size is constant (Aktipis, 2004; Smaldino and Schank, 2012) (but see Wakano et al., 2009). To vary movement rate, individuals move to an adjacent patch with various probabilities ( $= 10^{m-1}$  per time  $T$ , where  $m$  is log movement rate), and stay put if the chosen movement direction is across a boundary. Eight log movement rates were used, ranging from 0 to 0.7. Offspring are born into the parental patch and do not immediately disperse.

The non-spatial parameter values are:  $r = 0.1$ ,  $c = 0.01$ ,  $a = 0.05$ , and  $k = 0.1$ .  $r$  is decomposed into intrinsic birth rate (0.2) and death rate (0.1). Cooperation and competition ( $c$ ,  $a$ ,  $k$ ) occur between individuals within the same patch and affect the realized birth rate. These parameters satisfy the condition (Eq. (3)) for cooperation to causally increase population size ( $c/a < r/k$  translates to  $1/5 < 1$ ), so a null expectation is a positive association between cooperation and population size. This allows us to attribute a negative cooperation–population relationship to movement variation. For each measurement time step  $T$ , the simulation runs 100 times, with birth, death, and movement probabilities scaled by  $1/100$  to obtain an Euler approximation of the continuous-time dynamics (Eq. (1)). Realized movement rates were also measured to ensure conformity to model specifications (Fig. 2g–i). At each simulation step, birth and death events occur according to binomial probabilities defined by the life history parameters  $k$ ,  $r$ ,  $c$ ,  $a$  and the local densities of cooperators and defectors within each patch.

Cooperator frequency ( $P$ ) and population size ( $X$ ) were measured as averages obtained from  $T = 600$  to 1000 when the system stabilized (Fig. 2d–f). The Matlab code and simulation results are available on a Figshare repository (Tekwa et al., 2018). We capture

the local spatial conditions using relatedness (Hamilton, 1964; Lion and Gandon, 2010) and clustering coefficients, in order to further understand how movement rate affects cooperation. We first confirm in our simulations the generally accepted results that the correlational relatedness metrics  $R_c$  (relatedness between cooperators) and  $R_d$  (relatedness between defectors) (SM Appendix: Related Spatial Metrics) should be positively associated with cooperation (Hamilton, 1964; Lion and Gandon, 2010; Fisher et al., 2013; Tekwa et al., 2017). On the other hand, high clustering in one morph can limit its growth due to kin competition (Taylor, 1992; Wilson et al., 1992), leaving more space for the other morph to spread into and thus lowering its clustering. The difference  $C_{cc} - C_{dd}$ , or how much more cooperators cluster compared to defectors, should be negatively associated with cooperation under weak selection (Tekwa et al., 2017).  $C_{cd}$  (between morph clustering) should be negatively associated with cooperation assuming weak selection but is generally frequency-dependent (Tekwa et al., 2017).

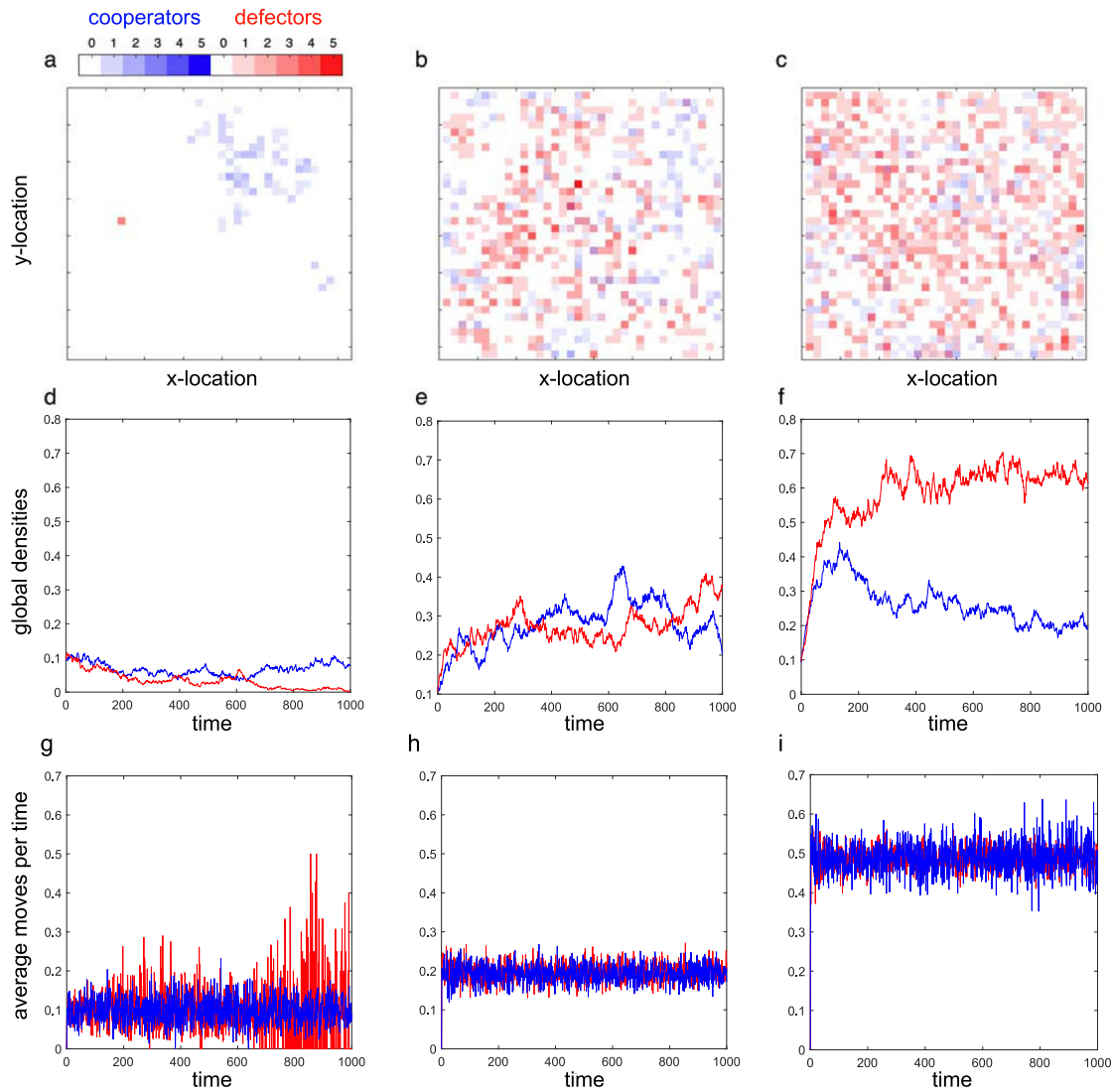
#### 3.2. Simulation results

Overall, we found that cooperator frequency correlates negatively with population size (Fig. 3a). ANCOVA (Table S1) showed that within each movement treatment, the cooperator frequency–population size relationships are positive (mean slope =  $0.24 \pm 0.023$  s.e.) (Fig. 3b), but the slopes are different ( $p = 3.2 \times 10^{-5}$ , Table S2). The slope increases with movement rate (Fig. 3c), indicating that cooperation more effectively increases population size when movement rate is high. This increase in the effectiveness of cooperation at the population level was masked by the strong selection against cooperation with increasing movement rate, as discussed next.

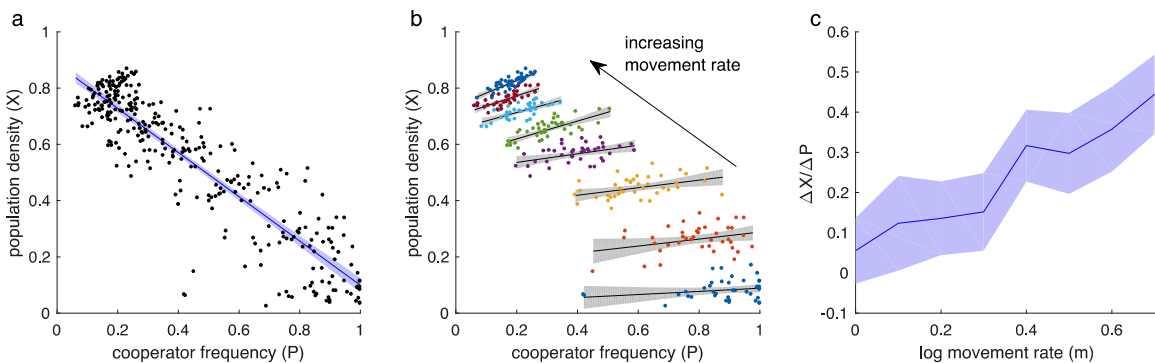
The negative overall relationship between cooperator frequency and population size is caused by movement rate. Movement rate increases population size but decreases cooperator frequency (Fig. 4a&b). Relatedness between cooperators ( $R_c$ ) and between defectors ( $R_d$ ) decreased with movement rates (Fig. 4c), which coincided with decreased cooperation as expected (Fig. 4b). At a microscopic spatial resolution, increasing movement rate led to slightly higher clustering between morphs, lower cooperator clustering, and much lower defector clustering. The difference  $C_{cc} - C_{dd}$  was negative at low movement rates, where defectors experiencing high clustering grew slowly because of kin competition, leaving more space for cooperators to colonize and thus lowering their clustering. Conversely,  $C_{cc} - C_{dd}$  was positive at high movement rates, where defectors successfully spread and decreased clustering due to superior intrinsic growth rate, leaving little space for cooperators to colonize and thus disproportionately increasing their clustering. We observed that the increase in  $C_{cc} - C_{dd}$  with movement rate (Fig. 4d) is negatively associated with cooperation (Fig. 4b) as predicted. The observed decrease in cooperator frequency with movement rate is also congruent with the increase in between-morph clustering.

### 4. Discussion

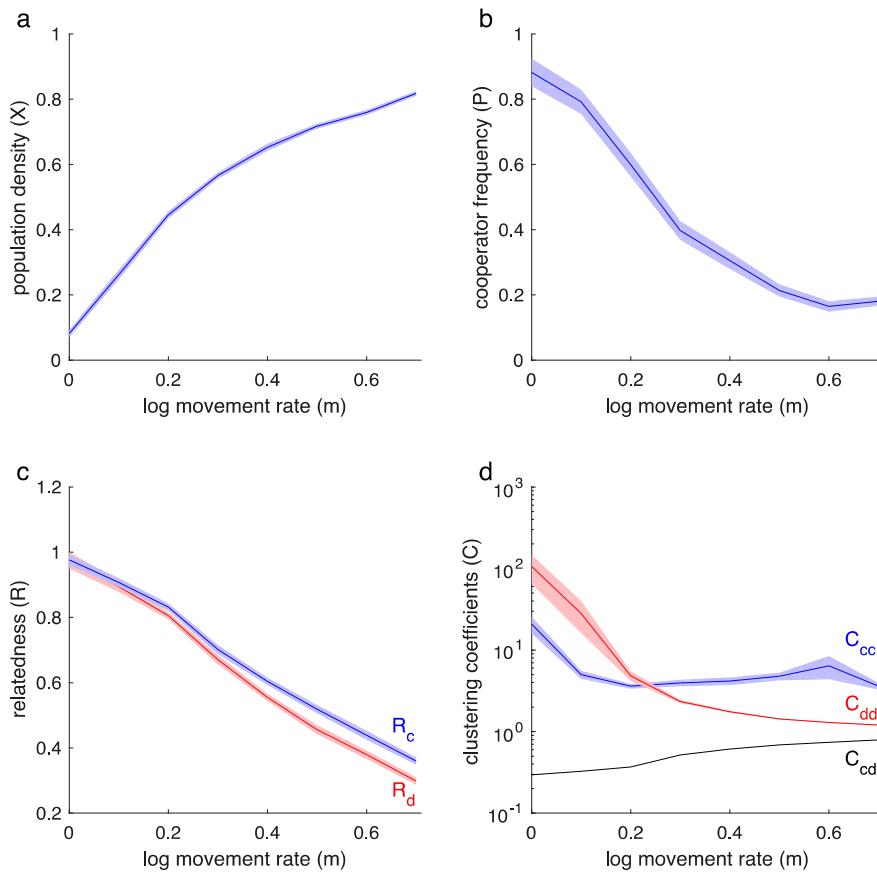
Our mathematical model and simulations show that increased cooperation between individuals can be negatively correlated with increased population size, even when cooperation by itself causally increases population size (Eq. (3)). This negative relationship is easily achieved even if cooperation bestows a net benefit to neighbours at low densities. When movement rate is low, relatedness is high and the difference between cooperator and defector clustering is low, which evolutionarily favours cooperators that locally experience lower per-neighbour competition (Eqs. (1) and (5)). However, such a population experiences greater total competition



**Fig. 2. Simulation snapshots.** **a–c.** Number of cooperators (blue) and defectors (red) within each patch of the  $36 \times 36$  grid (see top colour bar) at the end of simulations. Cells with both cooperators and defectors are depicted as mixtures of blue and red (purple). Log movement rates from left to right are  $m = 0, 0.3$ , and  $0.7$  for all rows. **d–f.** Global densities, or the average numbers per patch, of cooperators and defectors over time. **g–i.** Measured average moves across patches per cooperator or defector per time step. The expected moves per time step is  $10^{m-1}$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 3. Relationships between cooperator frequency and population density.** **a.** Overall relationship between cooperator frequency and population density ( $n = 320$ ,  $R^2 = 0.82$ ,  $slope = -0.79 \pm 0.021 s.e.$ ). **b.** Relationships within each log movement rate ( $m$ ) treatment, ranging from 0 at the bottom to 0.7 at the top in 0.1 increments ( $n = 40$  each). Scatter within particular scenarios are from random initial individual placements, movement, and birth/death stochasticity. **c.** Slopes of the cooperation–population relationships as a function of log movement rate (from **b**). Shaded bands are 95% confidence intervals.



**Fig. 4. Movement rate, relatedness, and clustering.** **a.** Effect of movement rate on total population density. **b.** Effect of movement rate on cooperator frequency. **c.** Relatedness between cooperators ( $R_c$ ) and between defectors ( $R_d$ ). **d.** Clustering coefficients ( $C_{ij}$ ), or how many times more likely that an individual of one morph ( $i$ ) encounters another morph ( $j$ ) than under well-mixed limit (null  $C_{ij} = 10^0$ ). Shades are 95% confidence intervals.

than a defective population in the limit of monomorphic (cooperator or defector only) populations (Eq. (4)). This cost of cooperation on population size can be understood as the ecological side-effect of kin competition, even though it may not impede the evolution of cooperation (Lion and Gandon, 2010; Van Dyken and Wade, 2012). As a result, the overall statistical cooperation–population relationship can be negative when comparing populations with controlled spatial variations (Fig. 1), even though cooperation directly increases population size (Fig. 4b) — a case of Simpson’s paradox (Simpson, 1951).

Our approach complements but contrasts from previous works that identified selection factors (Hamilton, 1964; Michod et al., 2006) or population outcomes (Hardin, 1968; Avilés, 1999; Avilés et al., 2002; Sanchez and Gore, 2013; Bateman et al., 2018) of cooperation without explicit individual-level spatial dynamics. Our results also differ from recent modelling work that incorporate evolutionary and demographic dynamics, which found positive cooperation–population relationships but did not consider differences between populations (Huang et al., 2015; Waite et al., 2015; Constable et al., 2016).

The negative cooperation–population relationship resembles what can be seen in games on graphs, where it was observed that when population size was increased (fixed from top-down), cooperator frequency decreased (Ohtsuki et al., 2006; Taylor et al., 2007). We did not consider this top-down causal direction from the population to cooperation, but rather assumed that individual interactions produce emergent population sizes (Fig. 1). A similar phenomenon was observed in a simulation study (Smaldino et al., 2013), where within a range of small global carrying capacities (imposed population size), increased population size was associated with a lower cooperator frequency. However, the same study

also found that when the global carrying capacity was sufficiently large (when top-down constraint relaxes), a further decrease in competition (larger imposed population size) was associated with a higher cooperator frequency. This positive trend agrees with our non-spatial partial derivative analyses on the effect of competition  $k$  (SM Appendix: Non-Spatial Parameters). These result comparisons suggest that top-down population size limits (rather than bottom-up competition) can be a source of negative cooperation–population relationship, but in its absence only variation in spatial clustering creates a negative relationship.

A negative cooperation–population relationship was also hypothesized in studies of environmental harshness, which did not directly invoke spatial clustering (Emlen, 1982). Simulation studies found that as the environment becomes harsher (growth rate  $r$  decreases), population size decreases and cooperator frequency increases (Smaldino et al., 2013). This disagrees with our partial derivative analysis on the pure effect of  $r$ , which affects both cooperation and population size in the same direction (SM Appendix: Eq. (S5)). The discrepancy can be explained by the apparent negative covariance between  $r$  and spatial clustering. Indeed, it is well established that arid landscapes produce patchy clustering patterns (Kéfi et al., 2007, 2008), which in turn can select for cooperation and produce a negative cooperation–population relationship.

A final example of a negative cooperation–population relationship arose in a spatial ecological public goods game (Wakano et al., 2009). It was observed that a decrease in cooperative benefit ( $a$ )-to-cost ( $c$ ) ratio favours cooperation and decreases population size. Our model suggests that decreased  $a$  or increased  $c$  should by themselves decrease both cooperator frequency and population

density. However, a low benefit  $a$  or high cost  $c$  was associated with a higher clustering through Turing pattern formation (Wakano et al., 2009; Kondo and Miura, 2010), which explains why cooperators are favoured when population size is small. The examples of Turing pattern and harshness illustrate that covariances between non-spatial parameters and spatial clustering, which we did not model but can arise either without (Wakano et al., 2009; Smaldino et al., 2013) or with coevolution (Koella, 2000; Rousset and Ronce, 2004; Aktipis, 2004; Le Galliard et al., 2005; Perc and Szolnoki, 2010), may lead to a negative cooperator–population size relationship. Our work provides a formal framework to analyse the relationship and suggests that it is not non-spatial parameters alone, but spatial clustering, that causes cooperative populations to be small.

A number of mechanisms can potentially circumvent the negative cooperation–population size relationship even as clustering varies between populations. We have already shown that less costly, more beneficial cooperation (Eq. (4)), or variations in non-spatial characteristics (Section 2.3) can create a positive cooperation–population size relationship. These non-spatial mechanisms can mask the opposing effects of space on cooperation and population size. Additionally, coordinated dispersal, such as seen in the cooperative fruiting-body formation in social amoeba (Strassmann et al., 2011), can potentially increase both cooperation and population size if local resources are depleted with use and recover slowly. This requires the explicit modelling of resource dynamics, which is a promising next step to further explore the robustness of the space-induced negative cooperation–population size relationship.

We know of no empirical example showing a negative cooperation–population relationship that can be directly attributed to spatial clustering. The causally positive relationship between cooperation and population size is consistently observed in experiments (Velicer, 2003; Chuang et al., 2009; Smith et al., 2010; Tekwa et al., 2017), but they did not deterministically vary spatial clustering. We believe that future experiments and observational data analyses will be able to demonstrate a negative cooperation–population relationship in two scenarios: (1) when common-pool resource cooperation is costly relative to carrying capacity and there is no spatial differentiation between morphs; (2) when movement rate or spatial clustering varies, populations with limited mobility will evolve higher levels of cooperation and smaller population size.

The theoretical results shed light on the hierarchy of biological organization (Keller, 1999; Okasha, 2006). Movement rate or spatial clustering can be understood to control the coupling between individual and population levels. When the levels are strongly coupled due to high movement rates or low clustering, the window for selection above the individual narrows and translates more strongly to the population level (Fig. 3c), but overall selection concentrates on the individual's ability to grow after frequent dispersal (hence favouring less investment in costly cooperation). When the levels are weakly coupled due to low movement rate or high clustering, the window for selection above the individual widens and translates weakly to the population level. In this case, overall selection favours local cooperation that does not align with population-level benefits. This interpretation is compatible with the evolutionary dilemma of cooperation, that higher-level selection is generally weaker than lower-level selection (Darwin, 1871; Hamilton, 1975; Axelrod and Hamilton, 1981; Levin, 2005). But we add to the thesis by explaining why cooperation, even when selected for, may not overcome a limited colonization rate to produce a net population size increase – an ecological dilemma of cooperation. Clearly, many highly-cooperative organisms such as ants and humans (Wilson, 1975) do overcome colonization limitations and produce large populations; our theory lays out possible conditions where cooperative populations are expected to be relatively small.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.tpb.2018.12.003>.

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