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Local densities connect spatial ecology to game, multilevel selection and inclusive fitness theories of cooperation[☆]

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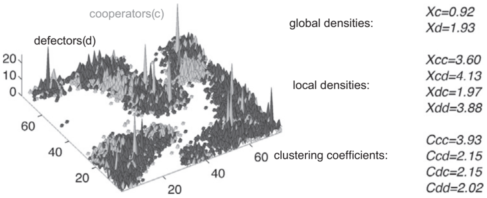
HIGHLIGHTS

- Local densities from spatial ecology capture cooperative interaction potentials.
- Price's equation identifies spatial and non-spatial selection mechanisms.
- Local densities form structure coefficient, contextual covariance, and relatedness.
- Local densities connect game, multilevel selection, and inclusive fitness theories.

GRAPHICAL ABSTRACT



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ABSTRACT

Cooperation plays a crucial role in many aspects of biology. We use the spatial ecological metrics of local densities to measure and model cooperative interactions. While local densities can be found as technical details in current theories, we aim to establish them as central to an approach that describes spatial effects in the evolution of cooperation. A resulting local interaction model neatly partitions various spatial and non-spatial selection mechanisms. Furthermore, local densities are shown to be fundamental for important metrics of game theory, multilevel selection theory and inclusive fitness theory. The corresponding metrics include structure coefficients, spatial variance, contextual covariance, relatedness, and inbreeding coefficient or *F*-statistics. Local densities serve as the basis of an emergent spatial theory that draws from and brings unity to multiple theories of cooperation.

1. Introduction

Cooperation is thought to play a crucial role in biological phenomena, including the rise of bacterial biofilms, eukaryotic cells, multicellular organisms, and societies (Maynard Smith and Szathmáry, 1999; Okasha, 2006). In the theories on the evolution of cooperation, as in many other complex subjects, there does not exist a universal theory that best explains all observed behaviours. Some non-spatial explanations include reciprocity (Trivers, 1971) and discrimination (Strassmann et al., 2011). Several theories invoke a role for space. Although space is certainly not the only important factor in the evolution of cooperation (Fletcher and Doebeli, 2009; Lehmann and Keller, 2006; Lehmann and Rousset, 2010; West et al., 2007), it is one of the most important (Débarre et al., 2014; Lion and van Baalen, 2008; Rousset and Ronce, 2004; Van Baalen and Rand, 1998).

Space is represented in different ways and described by a variety of metrics. These include structure coefficient (Tarnita

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et al., 2009), spatial variance (Wilson, 1977), contextual covariance (Heisler and Damuth, 1987), relatedness (Hamilton, 1964), and inbreeding coefficient or *F* statistics (Lehmann and Rousset, 2010), among others. But these metrics are not all purely spatial. It is thus important to identify a common language with which to measure and discuss spatial effects on cooperation, in order to discern when space really plays a role.

A recurrent discovery is that the evolutionary dynamics of cooperation in space can be modelled using pair densities (Débarre et al., 2014), or alternatively using the probabilities of identity between individuals (Rousset, 2002). These are then used to derive one of the five metrics we cite above. The discussions surrounding these terminologies remain encumbered by the highly technical mathematics and assumptions needed to mechanistically derive them, which include spatial moment approximation (Levin and Pacala, 1997), pair approximation (Matsuda et al., 1992), and quasi-equilibrium approximation (Débarre et al., 2014). If we are willing to take pair densities or probabilities of identity as quantities that can be measured and not necessarily mechanistically derived, then we may be able to open up the discussion of space and cooperation to empirical application. For this purpose, we will turn to the related and empirically applied metrics – local densities – which originate in neighbourhood models of plant interaction in spatial ecology (Pacala and Silander, 1985; Sapijanskas et al., 2013).

The purpose of this article is to present a coherent and comprehensive theoretical support for using a set of local densities as the central metrics in deciphering the spatial components of eco-evolutionary cooperation dynamics. First, we define local densities (Section 2.1) in precise terms, such that they can be empirically applied and incorporated into a dynamic model (Section 2.2). We then show that such a local interaction model can neatly distinguish the spatial and non-spatial selection mechanisms for cooperation (Section 2.3). By mathematically relating local densities to the current major paradigms, we can analyse when kin selection (Hamilton, 1964), group or multi-level selection (Wilson, 1977), and reciprocity (Trivers, 1971) refer to spatial, non-spatial, or partly spatial phenomena (Section 3).

There is an excellent theoretical synthesis on the various ways in which current major paradigms model space, and it is the immediate predecessor of our paper (Lion and van Baalen, 2008). Nevertheless, the previous synthesis used a more restrictive definition of local densities, which are used as pair densities in graphs with a predefined number of nodes. Our main task is thus to identify and establish a spatial metric that can be generally applied in both evolutionary and ecological contexts, in continuous or discrete space and graphs. Some additional novelties in our synthesis include: relating ecologically and game-theoretically motivated spatial models to the traditional concept of selection through Price's equation (Price, 1970); incorporating recent spatial evolutionary game developments (Tarnita et al., 2009); and relating spatial metrics to multilevel selection analyses (Okasha, 2006). Along the way, more familiar derivations are included to facilitate the transitions from one novel idea to the next, and to be inclusive, such that theoretical experts, empirical researchers, and any interested biologist can appreciate the generality and limitations of our model.

Our work does not adhere to a particular method of computing evolutionary fitness (see Tarnita and Taylor, 2014), or elucidate how spatial patterns arise (see Hamilton, 1964; Levin and Pacala, 1997; Matsuda et al., 1992). The local interaction model is not a complete synthesis; rather, it introduces a more general concept of local densities and strengthens the foundations of an ongoing spatial synthesis to include both traditional selection concepts and new dynamic theories.

2. Local interaction model

We begin with the concept of local density, which measures and models spatial interactions between individuals. Then we construct the general dynamic equations for the evolution of cooperation by adding terms for intrinsic growth rates and payoff functions. We conclude the section with an analysis of spatial and non-spatial selection mechanisms.

2.1. Local densities

We first introduce local densities as metrics that describes encounters, or interaction potentials in space, then we incorporate changes in local densities. These metrics were developed in the neighbourhood models of plant interactions (Bolker and Pacala, 1999; Levin and Pacala, 1997; Pacala and Silander, 1985), and are directly related to the pair densities (Matsuda et al., 1992) often used in cooperation theories (Débarre et al., 2014). We will carefully generalize these metrics for interacting individuals beyond plants.

Let us define a morph as a discrete trait or character that is heritable through survival or reproduction. We will call carriers of these discrete characters individuals. This definition of an individual is most applicable to haploid organisms, but can also be applied to individual genes, and to higher organisms if we adopt the phenotypic gambit (where the character inheritance of non-haploid organisms is assumed to approximate haploid inheritance – see Grafen (1984)). For each focal individual u across the entire population, we can measure the local density x_{uj} of morph j. Such local density is the number of morph j individuals weighted as a function of their distance from the focal individual. The local density of morph j around each individual u at location y_u in space

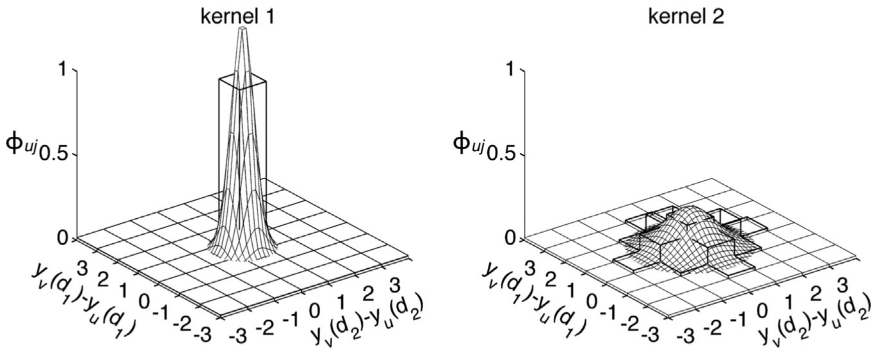

Fig. 1. A localized interaction kernel 1 versus a diffuse local interaction kernel 2. The smooth Gaussian mesh plots represent continuous-space kernels, while the bar plots represent discretized space approximation kernels, where spatial locations are defined at a lower resolution. y_u is the position of the focal individual (in dimensions d_1 and d_2), y_v is any position that may be occupied by other individuals, and ϕ_{uj} is the kernel weighting for the Euclidean distance $y_v - y_u$ from the focal individual.

is then:

$$x_{uj} = \sum_{v}^{\text{all } j \text{ indiv}} \varphi_{uj}(y_v - y_u) \tag{1}$$

The key to local density is the interaction kernel, i.e. the weighting function ϕ_{uj}. The interaction kernel is a probability density function, specifying the probability that a focal individual u interacts with a morph j partner v a distance $y_v - y_u$ apart. As a probability density function, ϕ_{uj} is positive and integrates to one over all possible distances. The shape of the interaction kernel implicitly models the intermediary spatial processes that affect fitness (fitness is defined later in Eq. (3)). Such processes may include the transmission of public goods (e.g. metabolites), information (e.g. warning calls), toxins, or at the simplest, physical boundaries or territories of individuals in contact-based interactions. Two symmetric interaction kernels, applicable in both continuous and discrete space, are illustrated in Fig. 1. We simplify the modelling problem by assuming that all individuals u of morph i experience their biotic environment through the same interaction kernel, ϕ_{ij}.

The expected value of x_{uj} over all individual u belonging to morph i, $X_{ij} = E[x_{uj}]$, is the average local density of morph j around morph i. X_{ij} can also be interpreted as morph i's encounter potential of morph j at a given time. We postulate that average local densities are the biotic neighbourhood variables affecting fitness. As the interaction kernel ϕ_{ij} becomes less localized (approaching a uniform function in space), the local density X_{ij} approaches the global density X_j, because then every neighbour is counted equally regardless of distance. The global density X_j is, by definition, the total number of individuals belonging to a morph per unit area globally, devoid of spatial information.

The average local density X_{ij} can deviate from the global density X_j, capturing the effect of clustering or segregation. The clustering between individuals of the same morph and the segregation from other morphs are spatial mechanisms that can favour cooperation, as we will see later.

Local densities are, in the spatial moment literature, functions of the second moment of the population distribution (Bolker and Pacala, 1997). The first moment is the global density. Thus, local density encapsulates the variance of the population distribution, and is analogous to local stochasticity in the structured population genetics literature (Rousset, 2004). We identify local densities, applicable in both continuous and discrete space, as the most general version of closely related concepts, such as pair densities or the environs (Matsuda et al., 1992), and probabilities of identity (Rousset, 2002). Pair densities $q_{i/j}$ are defined on graphs or lattices where each node can contain at most one individual, and express the probabilities that a randomly chosen neighbouring node of a morph i individual is of morph j. Thus, $q_{i/j}$ is simply X_{ij} when local densities are normalized by a predefined density ceiling (which is 1 in scenarios where pair densities apply). Probabilities of identity Q_x can be written as $q_{i/i}$, but are measured at a spatial scale denoted by x (such as within-deme and between-demes) and concern only the probabilities that two individuals are of the same morph i. Thus, local densities are more general: they allow us to use interaction kernels that may be diffused beyond immediate neighbours, and they capture morph-specific clustering relationships. In Section 3, we will revisit how these correspondences help us translate existing theories into the local interaction model.

Over many generations, the spatial distribution of individuals changes due to birth, death, natal dispersal and migratory movement. In Fig. 2, we illustrate how such spatial dynamics affect local densities in a hypothetical system of cooperators and defectors (see Appendix A). Birth, limited natal dispersal, and chemotactic movement (tendency to come together) increase spatial clustering, whereas death and random movement lead to thinning. We can relate average local densities to global densities through the clustering coefficient C_{ij} (defined at t to emphasize possible time dependence):

$$X_{ij}(t) = C_{ij}(t) X_j(t) \tag{2}$$

X_{ij} should be positively correlated to X_j – if there are more individuals of morph j, they will probably be encountered more often by any morph i even without spatial structure. By taking out this default correlation, clustering coefficients (i.e. normalized local densities) reveal clustering levels beyond mean-field expectations. When the clustering coefficient C_{ij} is greater than one, morph j tends to cluster around morph i individuals more than would be expected if individuals were distributed uniformly. Note that $X_{ij}X_i = X_{ji}X_j$, because the average number of ij pairs from either the i or j perspective is the same. By substitution, $C_{ij}X_jX_i = C_{ji}X_iX_j$, thus $C_{ij} = C_{ji}$. Clustering coefficients are convenient ratios with which to interpret within-morph and between-morph clustering patterns. Even though local densities and clustering coefficients can change over the course of evolution (Fig. 2), for most of our discussion we will use them as values from the population's equilibrium where evolutionary success is often calculated.

2.2. General dynamic equation and payoff function

In the general dynamic equations that describe how a cooperative population evolves, the response variable of interest is the per capita growth rate, i.e., the per capita rate of change in the global density of each morph, which we define as fitness. But we emphasize the dynamics of fitness, because the biotic environment – the local densities – changes through the course of evolution. We thus relate per capita growth rates of S number of

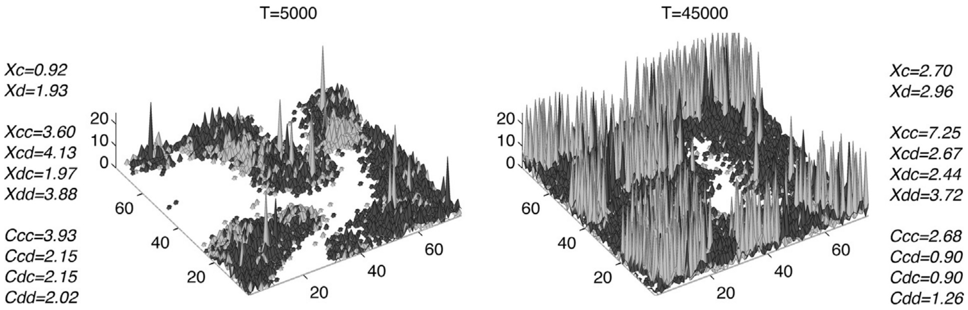

Fig. 2. An example of cooperator (subscript c) and defector (subscript d) spatial distributions, illustrated as local peaks in light and dark at two time points. Between time $T = 5000$ and $T = 45{,}000$, global population densities (X_c and X_d), average local densities (X_{cc}, X_{cd}, X_{dc}, X_{dd}), and clustering coefficients (C_{cc}, C_{cd}, C_{dc}, C_{dd}) change. The individual-based simulation is based on the production and consumption of an underlying diffusible public good on a 75×75 spatial grid. Both individuals and public good move in density-dependent fashions, leading to cluster formations (see Appendix A). Local densities and clustering coefficients were computed using kernel 2 in Fig. 1.

morphs to average local densities in the following form:

$$\frac{dX_i}{X_i dt}(t) = r_i + f_i(X_{i1}(t), X_{i2}(t), \ \dots \ , X_{iS}(t)) \tag{3}$$

Eq. (3) is the local interaction model, which states that the per capita growth rate depends on a constant r_i, the intrinsic growth rate, and a function f_i containing local densities. r_i is called the intrinsic growth rate because it does not depend on densities. f_i can be called the payoff function (Hofbauer and Sigmund, 2003), which can be non-linear. Such a density-based model by itself does not assume a finite population size, but does account for the discreteness of individuals (Durrett and Levin, 1994; Levin and Pacala, 1997), a character that is important in realistic spatial models. The model concentrates on the effect of selection, in contrast to finite-population models where mutation and drift are important (Tarnita and Taylor, 2014). To explicitly incorporate drift, one can work with a stochastic version of Eq. (3). The main advantage of Eq. (3) is that it allows for a simple mathematical treatment of spatial demographic dynamics without necessarily assuming a model-imposed (rather than emergent) population ceiling or a movement/dispersal pattern restricted by simulation update rules. The parameters can therefore be easily estimated either from time series or independently. As a differential equation, Eq. (3) also represents a concise mathematical form that can approximate the dynamics of other model systems, and will facilitate the identification of common terms across different theories.

From global densities, we get the frequency, or relative proportion, of each morph, $p_i = X_i/X$, where X is the total population density. Further, in a 2-morph population, if morph 1 is assigned a character value of 1, and morph 2 a character value of 0, then p_1 (written as p when it is clear) is just the average morph character z of the population. Traditionally, z is understood as the evolutionary state. dz/dt (or equivalently dp/dt) is the change in morph character, i.e., the evolutionary change.

There are several features of the payoff function that are crucial to cooperation. If the payoff function f_i is an increasing function of X_{ij}, then morph j provides a net benefit to morph i. f_i can be nonlinear, as there can be regimes where cooperation dominates, and others where competition dominates. This idea has been developed in population ecology as the Allee effect (Allee, 1931; Courchamp et al., 1999). Nonlinearity allows us to account for the fact that individuals simultaneously possess multiple cooperative and competitive traits or characters that are amplified at different environmental states. Further, if $f_1 \neq f_2$, then morphs 1 and 2 are said to have asymmetric payoff functions. That is, different morphs may be affected differently by the same biotic environment.

In summary, our model incorporates three components for the evolution of cooperation: intrinsic growth rates (r_i), payoff functions (f_i), and local densities (x_{ij}). Next, through a simpler analytical model, we analyse what these components mean in the Darwinian language of selection.

2.3. Selection for cooperation

The three components introduced above can be funneled into general classes of selection mechanisms. We need to transform the equations for morph density change (Eq. (3)) into ones for morph character change. Price's (1970, 1972) equation is one way of performing such a transformation, which has the advantage of being central to multilevel selection analysis, as we will see. Here we use a continuous-time version, which is just an application of the chain rule from calculus (Day and Taylor, 2003; Walker, 2012), to analyse the change in the average individual character of a population $dz(t)/dt$ at a given time t. The equation is

$$\frac{dz(t)}{dt} = cov(w_u, z_u) \tag{4}$$

where w_u is the fitness of an individual u, and z_u is the character value of that individual. On average, w_u is just the per capita growth rate of the individual's morph given the set of average local densities experienced at time t (Eq. (3)).

In the following analytical example, we consider two morphs that have different intrinsic growth rates. In addition, morph 1 provides help, from which the two morphs benefit differently. This evolutionary scenario may be expected of a cooperative trait (possessed by morph 1) – the production of a costly local public good. Here we ignore the effect of competition and payoff function non-linearity. The fitness of morph i can then be simplified to the following equation:

$$\frac{dX_i}{X_i dt}(t) = r_i + a_{i1} X_{i1}(t) \tag{5}$$

A positive a_{i1} indicates helping by morph 1. But Eq. (5) expresses the fitness of a morph and not of an individual. To obtain w_u, let us define the fitness of an individual u in term of character value z_u; let $z_u = 1$ be the character value of an individual of morph 1, and $z_u = 0$ be the character value of an individual of morph 2. We can then write an individual u's intrinsic growth rate as $r_u(z) = r_2 + (r_1 - r_2)z_u$, and payoff function as $a_{u1}(z) = a_{21} + (a_{11} - a_{21})z_u$. From here, we can write down the fitness of an individual u, which depends on its morph and on its local density x_{u1} at time t:

$$w_u = r_2 + (r_1 - r_2)z_u + (a_{21} + (a_{11} - a_{21})z_u)x_{u1} \tag{6}$$

Note that for $z_u = 1$, Eq. (6) gives the fitness of morph 1 ($r_1 + a_{11}x_{11}$); and for $z_u = 0$, Eq. (6) gives the fitness of morph 2 ($r_2 + a_{21}x_{21}$). By substituting Eq. (6) into the covariance Eq. (4), we obtain the change in the population's average character:

$$\begin{aligned}\frac{dz(t)}{dt} &= cov(r_2 + (r_1 - r_2)z_u + (a_{21} + (a_{11} - a_{21})z_u)x_{u1}, z_u) \\ &= \overbrace{(r_1 - r_2)var(z_u)}^{[1]} + \overbrace{a_{21}cov(x_{u1}, z_u)}^{[2]} + \overbrace{(a_{11} - a_{21})cov(z_u x_{u1}, z_u)}^{[3]}\end{aligned} \tag{7}$$

This equation identifies 3 distinct selective forces at a given time, each of which consists of a selection coefficient and a variance or covariance term—a potential for selection. Term [1] points to the non-spatial selection due to the intrinsic growth difference between morphs 1 and 2, which is amplified by the character variance in the population. Term [2] accounts for the selection for cooperation due to purely spatial effects. That is, the basic amount of benefit that both morphs obtain from encounters with morph 1 (a_{21}) contributes to the disproportionate increase in morph 1, if morph 1 individuals tend to cluster (high x_{u1} for u belonging to morph 1) and segregate from morph 2 (low x_{u1} for u belonging to morph 2). Term [3] accounts for the non-spatial selection for cooperation due to payoff function asymmetry. Since $\mathrm{cov}(zx_{u1}, z) > 0$ by the definition of covariance, the selection term [3] is positive as long as morph 1 benefits more from interaction with the helper (morph 1) than morph 2 does.

We have thus demonstrated that the evolution of cooperation acts through selection on one or more of the following mechanisms: intrinsic growth, space, and payoff function asymmetry. More mechanisms subject to selection can be easily identified by analysing a more complex payoff function. For instance, if we consider effects that result from interactions between morphs, then the between-morph local density x_{12} would become part of the spatial selection potentials. In connecting local densities to the language of selection, Eq. (7) constitutes a novel technical contribution.

3. Relations to other evolutionary theories

We will now establish the formal correspondence between local densities and metrics in evolutionary game theory, multilevel selection theory, and inclusive fitness theory.

3.1. Evolutionary game theory

Game theory has been employed to understand cooperation, first in human society (Von Neumann, 1928), and later in the evolution of other organisms (Maynard Smith and Price, 1973). We will develop the basic game formalism and focus on the classical Prisoner's Dilemma as an example. Then, we will discuss two mechanisms that game theory has proposed to explain the evolution of cooperation, i.e. non-spatial reciprocity and spatial reciprocity, and interpret them in terms of payoff function and local densities.

In a round of game, an individual (actor) interacts with another individual (partner) according to the partner's global morph frequency, gaining or losing fitness according to a payoff matrix with constant interaction coefficients. For a 2-player game, the payoff matrix A is

$$A = \begin{array}{cc} & \textit{partner} \\ & \begin{array}{cc} 1 & 2 \end{array} \\ \textit{actor} & \begin{array}{c} 1 \\ 2 \end{array} \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \end{array} \tag{8}$$

One simple condition commonly used for the selection of morph 1 over morph 2 is the strict Nash condition (Nowak, 2006a): $a_{11} > a_{21}$. Even though other payoff terms contribute to determine precise evolutionary trajectories, we will begin with the strict Nash condition, which also implies the evolutionary stable condition (Maynard Smith and Price, 1973).

The Prisoner's Dilemma is the case where morph 1 is the cooperator, morph 2 is the defector, and $a_{21} > a_{11} > a_{22} > a_{12}$. The game prevents the strict Nash condition for morph 1. This is the toughest game for cooperation because cooperators are exploited by defectors, even though the best outcome for the population is for all to cooperate.

We can derive the non-spatial game equation as a special case of the local interaction model. The three traditional game assumptions, interpreted through our model, are: (1) the payoff functions are linear functions of relative morph densities (or frequencies), (2) the total population size does not matter (no demographic feedback), and (3) intrinsic growth rates are identical between morphs. It can be readily shown that the payoffs a_{ij} in game theory are the coefficients of linear payoff functions in the local interaction model (Appendix B). It follows that the Prisoner's Dilemma must involve payoff function asymmetries ($a_{21} \neq a_{11}$, $a_{22} \neq a_{12}$). For other important types of cooperative games such as the Snowdrift Game and pseudo-reciprocity (Clutton-Brock, 2009), the underlying payoff orders are different but still retain the basic feature that they can be expressed as payoff function asymmetries. While these games are perhaps theoretically less curious because no augmenting terms are needed for cooperation to evolve, they are more common in nature (Connor, 2010).

Non-spatial reciprocity can solve the Prisoner's Dilemma. Trivers (1971) postulated that if individuals change their behaviour, or reciprocate, depending on the history of their interactions in repeated games, they can change the game payoffs such that cooperators are favoured. For example, the famous tit-for-tat strategy of cooperators (morph 1) versus defectors (morph 2) in a non-spatial iterated Prisoner's Dilemma game (Axelrod and Hamilton, 1981) is one that modifies payoffs (Taylor and Nowak, 2007) as

$$A = \begin{bmatrix} \frac{a_{11}}{1-\rho} & a_{12} + \frac{\rho a_{22}}{1-\rho} \\ a_{21} + \frac{\rho a_{22}}{1-\rho} & \frac{a_2}{1-\rho} \end{bmatrix} \tag{9}$$

ρ is the probability that an individual continues interacting with a particular partner, and a_{ij} are the payoffs if there were no repetition of the game. There exists a ρ such that the cooperative strategy in a Prisoner's Dilemma is a strict Nash equilibrium (would be selected for), i.e. $a_{11}/(1-\rho) > a_{21} + \rho a_{22}/(1-\rho)$. For the same reason that game can incorporate nonspatial reciprocity – and the implied association through discrimination – by modifying payoffs, the local interaction model does the same through payoff functions. This leaves local densities to capture purely spatial effects.

The second solution to the Prisoner's Dilemma incorporates space into game theory (Nowak and May, 1992), resulting in spatial reciprocity (Nowak, 2006b). The intuition is the same as what we gained from our model: clustering between cooperators can allow cooperation to evolve. Today, many spatial games are built from simulations on a lattice or graph, with a total population size that either does (Lion and van Baalen, 2008) or does not change (Tarnita et al., 2009). We will first introduce a novel formulation of spatial game that adheres more closely to the tradition of game and reciprocity theories. Then we will highlight the connections between existing spatial game formulations and local densities.

We begin with a bilinear version of the local interaction model, the spatial Lotka–Volterra model (Matsuda et al., 1992), which is (Appendix B)

$$\frac{dX_i}{X_i\,dt} = r_i + \sum_{j=1}^{2} a_{ij} X_{ij} \tag{10}$$

By assuming no intrinsic growth difference we can arrive at a spatial game formulation that is analogous to the non-spatial game (see Appendix B). In term of clustering coefficients, the modified 2-player payoff matrix becomes:

$$A = \begin{bmatrix} C_{11}(t)a_{11} & C_{12}(t)a_{12} \\ C_{21}(t)a_{21} & C_{22}(t)a_{22} \end{bmatrix} \tag{11}$$

C_{ij} is the time-dependent clustering coefficient between morph i and morph j as introduced before (and $C_{12} = C_{21}$). When the coefficient is larger than one, there is clustering, which amplifies the interaction between the morphs i and j. By analogy to non-spatial reciprocity, if the clustering coefficients are constants, there exists augmenting terms, C_{11} and C_{12}, such that the cooperative strategy in a Prisoner's Dilemma is analogous to a strict Nash equilibrium (would be selected for), i.e., $C_{11}a_{11} > C_{21}a_{21}$. In general, however, clustering coefficients may be time-dependent, in which case the selection condition may differ.

A more prevalent type of cooperation in nature, by-product mutualism (Connor, 2010), is often implicitly associated with a spatial component – morph 2 intentionally approaches morph 1 to increase the benefit received (a_{21}) while also providing help (i.e. a positive a_{12}). By-product mutualism is in fact a type of spatial game, where C_{21} in particular is raised above 1. Again, it is instructive to view the spatial effect as augmenting the underlying payoffs (i.e. the term $C_{21}a_{21}$).

In current game models that incorporate space explicitly and assume constant and finite population size, nodes are always occupied by an individual of one morph or another (Ohtsuki et al., 2006; Taylor et al., 2007). The appropriate selection condition for such a game in the limits of low mutation rate and weak selection is when the fixation probability of morph 1 is greater than that of morph 2 (Tarnita et al., 2009). The effect of the graph can be summarized through a single structure coefficient σ (Allen et al., 2013; Débarre et al., 2014; Tarnita et al., 2009). This coefficient enters the selection condition as

$$\sigma a_{11}+a_{12}>a_{21}+\sigma a_{22} \tag{12}$$

While the structure coefficient above is not purely spatial because it incorporates the effect of competition from the game update rules on graphs, we can look for something corresponding to σ in our model. An analogous condition for our density-based model is found by looking at whether the change in cooperator frequency around $p=1/2$ is positive. From the local interaction model (Eq. (11)), we easily rediscover Eq. (12). We find that for a saturated habitat, $\sigma=X_{ii}/X_{ij}$ (see Appendix C) or, equivalently, $\sigma=C_{ii}/C_{ij}$ (where $i\neq j$). This result parallels the finding of evolutionary set theory (Nathanson et al., 2009), which allows for overlapping interaction kernels between individuals and a form of dynamic graph but which, nevertheless, assumes a constant population size. In evolutionary set theory as in the local interaction model, σ is purely spatial. This novel analogy between spatial game and the local interaction model indicates that, given fully specified payoff functions in a saturated habitat, clustering within morph and segregation from the other morph will generally favour within-morph cooperation.

In spatial games with non-constant population size, the effect of space cannot be captured by a single coefficient (e.g. Lion, 2009). In Appendix D, we demonstrate how the dynamic formulation in such a spatial game model of cooperation (Van Baalen and Rand, 1998) corresponds to our model. It is interesting that locally at each game step, the spatial game involves linear payoffs. However, the rules of the game, including the possibility of empty space, result effectively in nonlinear (quadratic) payoff functions.

We have used the local interaction model to derive results that parallel those in existing evolutionary games. Both non-spatial and spatial reciprocity can be viewed from a game perspective as similarly augmenting payoffs to favour cooperation. These directly correspond to changes in payoff function asymmetry and changes in local densities.

3.2. *Multilevel selection theory*

Various models of the evolution of cooperation have been built from the group or multilevel selection perspective. The key postulate is the existence of higher levels of organization in which interactions among individuals occur. We will interpret the concepts of group selection and the contextual analysis – a multilevel selection analysis – using our model.

We refer to group selection as a special case of multilevel selection where only two biotic levels exist: individuals and non-overlapping groups. The most widely cited modern group selection model is the structured deme model (Wilson, 1977; Szathmáry and Maynard Smith, 1997; Loreau, 2010), where interaction occurs within localized "trait groups" (or simply groups) but reproduction and natal dispersal are within the larger deme. The structured deme model captures the conflict between the relative fitness of individuals within groups and the relative fitness of groups. Its status as a special case under our model is explored in Appendix E. In essence, group selection postulates that a set of group characters (denoted Z_u) affects the individual u belonging to that group. We show that Z_u is the local density x_{u1} within groups of 2 morphs, where the interaction kernel defines a uniform interaction probability within individual u's group. Wilson's (1977) popular model assumed that payoff functions are symmetric. The group selection metric of spatial variance that describes cooperator clustering can be translated into average local densities (see Appendix E).

A more general method for partitioning selection into lower- and higher-level selections (or into within- and between-group selections) is the contextual analysis, a method borrowed from sociology (Heisler and Damuth, 1987) and is related to Price's (1970) equation. Contextual analysis breaks down the causes of evolution into individual-level selection (the selection coefficient associated with the variance in individual characters) and higher-level selection (the selection coefficient associated with the (contextual) covariance between the individual character and a higher-level character) (Appendix F). Most simply and perhaps most satisfyingly, a higher-level character can be considered anything that cannot be predicted by the variance in individual character alone (Okasha, 2006).

We can analyse a two-morph version of the local interaction model using the contextual analysis. For clarity, we only consider payoff functions that are linear but asymmetric between two morphs. Further, only a_{11} and a_{21} are non-zero (only morph 1 affects others' fitness). Thus, fitness is just as we defined in Eq. (5). The change in the average individual character is written in Eq. (7).

We can partition the right-hand side of Eq. (7) into levels of selection according to the variance and contextual covariance terms. In term [1] of Eq. (7), r_1-r_2, or intrinsic growth difference, is an individual-level selection coefficient because it is associated with the variance in individual character. This variance can be predicted by observing the individual character alone.

On the other hand, the covariance term [2] in Eq. (7) cannot be predicted by the individual character alone. Term [2] states that even if two morphs respond identically to the same biotic environment, one morph can experience positive selection if it tends to experience a higher local density. The portion of the payoff function that the two morphs share (a_{21}) constitutes the corresponding higher-level selection coefficient. Term [2] encapsulates the traditional group selection mechanism as introduced at the beginning of this section.

Term [3] in Eq. (7), the payoff function asymmetry, is more complex. Its covariance can be partitioned as shown in Appendix F:

$$X_{\bullet 1}\mathrm{var}(z_u)+(1-z)\mathrm{cov}(x_{u1},z_u) \tag{13}$$

$X_{\bullet 1}$ is the average local density of morph 1 around any individual. By substituting Eq. (13) into Eq. (7) and grouping terms by variance and covariance, we obtain the following equation for evolutionary change:

$$\frac{dz}{dt}=\left[(r_1-r_2)+\boxed{(a_{11}-a_{21})X_{\bullet 1}}\right]\mathrm{var}(z_u)+\left[a_{21}+\boxed{(a_{11}-a_{21})(1-z)}\right]\mathrm{cov}(x_{u1},z_u) \tag{14}$$

Eq. (14) says that payoff function asymmetry affects both levels of selection (see boxed terms).

Since the individual-level selection term (Eq. (14)) contains the average local density $X_{\bullet 1}$, it cannot be predicted by the individual characters alone. On the other hand, $X_{\bullet 1}$ is independent of the individual character at a given time. We may call $(a_{11}–a_{21})X_{\bullet 1}$ an interaction between individual and higher-level selections, since in a dynamic sense higher-level characters do affect $X_{\bullet 1}$. It is not entirely surprising that there is not a one-to-one mapping between mechanisms and levels of selection, as there are many possible selection mechanisms, while our use of contextual analysis only identifies two levels. This multilevel selection partitioning of spatial and non-spatial effects is a novel contribution.

To summarize, group selection theory emphasizes the importance of spatial group formation in the evolution of cooperation. Multilevel selection more generally identifies intrinsic growth differences as individual-level selection, and the difference in morphs' experienced average local densities as higher-level selection (in particular as traditional group selection). On the other hand, payoff function asymmetry straddles two levels of selection, suggesting that biotic levels are not cleanly segregated under the local interaction perspective.

3.3. *Inclusive fitness theory*

Inclusive fitness theory, including kin selection mechanisms (Hamilton, 1964), is individual-centred. It includes fitness effects on others as part of the actor's fitness, weighted by relatedness (hence the term inclusive fitness). This individual-centred formulation necessitates identifying cost to self (direct fitness effect) and benefit to others (indirect fitness effect). We will show how these features, as well as Wright's F statistics (Wright, 1949), relate to the local interaction model, thereby reinforcing known but often convoluted links between inclusive fitness theory, spatial population genetics, and spatial ecology in a novel way.

Inclusive fitness can be derived from standard population genetics (Appendix G). For a two-morph population in which individuals affect interacting partners equally within an interaction scale, we arrive at the following equation describing changes in morph 1 frequency:

$$\frac{dp}{dt} = p(1-p)(r_1 + R_1 X_{1\bullet} b_{1\rightarrow\bullet} - r_2 - R_2 X_{2\bullet} b_{2\rightarrow\bullet}) \tag{15}$$

$b_{1\rightarrow\bullet}$ is the benefit given by a morph 1 individual to a partner on each encounter without discrimination. The total benefit given by an individual of morph i to its neighbours is then $X_{1\bullet} b_{1\rightarrow\bullet}$. The difference between the intrinsic growth rates, r_1–r_2, emerges as the intrinsic cost to morph 1. This difference is also known as a direct fitness effect. There are two relatedness terms, R_1 and R_2, which are dimensionless ratios of global frequency and local densities (Appendix G):

$$R_1 = \frac{X_{11}/X_{1\bullet} - p}{1-p}, \quad R_2 = \frac{X_{21}/X_{2\bullet} - p}{-p} \tag{16}$$

Relatedness can be interpreted as describing interaction neighbourhoods. If there are more morph 1 individuals in a morph 1 neighbourhood ($X_{11}/X_{1\bullet}$) than globally (p), R_1 is positive. An associated positive benefit $b_{1\rightarrow\bullet}$ would then contribute positively to morph 1's relative inclusive fitness. If there are fewer morph 1 individuals in a morph 2 neighbourhood ($X_{21}/X_{2\bullet}$) than globally (p), R_2 is positive. But any associated positive benefit $b_{2\rightarrow\bullet}$ counts against morph 1's relative inclusive fitness, because then the fitness of morph 2 is raised more than that of morph 1. Such relatedness metrics capture the spatial kin selection mechanism. From our derivation (Appendix G), we find that the benefit given by j is the same as the payoff (or linear payoff function) that any individual gets when encountering morph j: $b_{j\rightarrow\bullet} = a_{\bullet j}$. For a 2-morph population, the equality implies the following constraints: $a_{11} = a_{21}$, $a_{22} = a_{12}$, i.e., payoff function symmetry.

Relatedness has been linked to Wright's F statistics, which are based on probabilities of identity. Probabilities of identity are also known as pair densities when they are not conditional on the individuals' morphs (Débarre et al., 2014). In Wright's island model, (Lehmann and Rousset, 2010; Rousset and Billiard, 2000), the probability of fixation of cooperation is determined by F_{ST} in place of relatedness. This substitution hinges on the assumption of weak selection, such that we only have to consider the change in frequency near $p = 1/2$. With the additional restriction that within-morph clustering is unconditional ($C_{11} = C_{22}$), we show in Appendix H that F_{ST} is identical to R_1. This equality links the theory of evolution of cooperation based on local densities to the classic subdivided population literature and coalescence theory (Rousset and Billiard, 2000).

In inclusive fitness theory, payoff function asymmetry surfaces in the forms of kin and kind discriminations (Strassmann et al., 2011) and the green beard effect (Gardner and West, 2010). These are non-spatial mechanisms whereby benefits are given discriminately towards an individual's own morph. We call these collectively helping by discrimination. Through discriminated helping, the fitness of each morph is affected differently given the same type of encounter, thus it is a scenario of payoff function asymmetry. Rather than expressing helping by discrimination in term of payoff function (or cost and benefit), inclusive fitness theory expresses discrimination through high relatedness (Gardner and West, 2010). In other words, in the case of payoff function asymmetry, relatedness is a compound of spatial and non-spatial mechanisms.

To see how we may modify inclusive fitness to decipher spatial and non-spatial mechanisms, we will consider both plastic cost and discriminated benefit (Appendix G). A plastic cost (c_{ij}) is one that is only incurred by an actor of morph i when morph j is encountered. A discriminated benefit from a morph i individual ($b_{i\rightarrow j}$) is one that is only received by a partner of morph j. In Appendix G, we show that by specifying the target morph that receives a certain benefit, Eq. (15) becomes:

$$\frac{dp}{dt} = p(1-p)(r_1 + (b_{1\rightarrow 1} - c_{11})X_{11} + (b_{2\rightarrow 1} - c_{12})X_{12} - r_2 - (b_{1\rightarrow 2} - c_{21})X_{21} + (b_{2\rightarrow 2} - c_{22})X_{22}) \tag{17}$$

It can be shown (Appendix G) that Eq. (17) is equivalent to the spatial Lotka–Volterra Eq. (10) – a case of the local interaction model, through the following identity:

$$b_{j\rightarrow i} - c_{ij} = a_{ij} \tag{18}$$

This equality completes the correspondence between the payoff function terms of inclusive fitness theory, the local interaction model (Eq. (5)), evolutionary game (Eq. (8)), and multilevel selection (Eq. (14)).

4. Discussion

We began our investigation by proposing local densities X_{ij} (Eq. (1)) as the central metrics describing the spatial structure of cooperative populations, incorporating within-morph (subscripted ii) and between-morph (subscripted ij) clustering and segregations. Using the appropriate interaction kernel, local densities capture interaction potentials. Clustering coefficients C_{ij} (Eq. (2)), which are ratios of local densities over global densities, prove to be useful numbers to consider: when they are above one, they indicate clustering. Using the local interaction model based on local densities in conjunction with Price's equation, we identified three selection mechanisms in a novel way (Eq. (7)). These include selections due to intrinsic growth rate difference, to spatial effects, and to payoff function asymmetry – or how different morphs are differently affected by interactions.

Using analyses based on local densities, we uncovered some new connections between evolutionary game theory, multilevel selection theory, and inclusive fitness theory. In evolutionary game theory, assuming habitat saturation, the recently developed structure coefficient σ (Tarnita et al., 2009) (Eq. (12)) can be written as a composite of local densities or clustering coefficients: $\sigma = X_{ii}/X_{ij} = C_{ii}/C_{ij}$. In multilevel selection theory, higher level selection corresponds to the selection potential as represented by cov(x_{u1}, z_u), or the covariance between the local density of the helper morph as experienced by individual u and the morph z of that individual (Eq. (14)). In inclusive fitness theory, assuming no kin discrimination and a sole helper morph 1, relatedness is a function of local densities: $R_1 = (X_{11}/X_{1\bullet})/(1-p)$ (Eq. (16)). Finally, the fitness effect coefficients found in the different theories can be summarized as payoff function by the relationship $b_{j\rightarrow i} - c_{ij} = a_{ij}$

(Eq. (18)). Such an expression can also capture non-spatial kin discrimination, as discrimination is a form of payoff function asymmetry (where different morphs i gain differential payoffs from the same interacting partner j).

Local densities can be viewed as a technical means (in the forms of pair densities or probabilities of identity) to obtaining existing composite metrics such as structure coefficient, higher level selection potential and relatedness. However, they can also be viewed as major variables of interest, on par with population density and morph frequency, all of which are interlocked in eco-evolutionary feedbacks. Local densities are ecologically intuitive metrics describing different kinds of clustering, and they clearly partition spatial versus non-spatial effects in the evolution of cooperation. They are measurable quantities in continuous or discrete space and graphs, can incorporate nuanced modelling of interaction kernels or scales, and allow for fully emergent demographic dynamics without pre-defined limits. Through local densities, we have further strengthened the increasingly apparent links between spatial ecology and evolutionary theories (Lion and van Baalen, 2008). We hope to have highlighted the value of the common vocabularies that biologists use to formalize cooperation.

The local interaction model is not a replacement of current theories. Rather, it brings unity and focus to the spatial aspect of existing evolutionary theories of cooperation. In favour of clarifying spatial metrics used to construct evolutionary equations, important aspects were left out. For example, there are different ways to evaluate the ultimate evolutionary success of cooperators or a cooperative trait, including evolutionary stability (Maynard Smith and Price, 1973), fixation probability, and inclusive fitness effect (Tarnita and Taylor, 2014). In our work, we have mostly discussed the changes in cooperator frequency (p) or cooperative character (z), except when we utilize fixation probability in comparing our model with the structure coefficient (σ) and F statistics (F_{ST}). Since change in frequency and character are only indicative of evolutionary directions at a given state, before accounting for mutation, we maintain generality but without specifying how to obtain long-term evolutionary trajectories. As well, there are different ways to derive the changes in spatial interaction patterns through identity by descent and family structure (Hamilton, 1964), life history and demography (Lehmann and Rousset, 2010), and update rules and graph topologies (Débarre et al., 2014), among others – which we did not elaborate on. The measure of evolutionary success and the mechanistic understanding on pattern formation are crucial, but in principle they can be expressed through models based on local densities.

We have demonstrated that local densities are general and common spatial metrics across major theories of the evolution of cooperation. For both empirical and theoretical investigations, local densities are technically precise and intuitive vocabularies that can sharpen our understanding of the role of space in maintaining cooperation.

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Appendix A. Simulation

To illustrate how local densities and clustering coefficients develop, we simulate a complex public good game. Individuals are either cooperators, who produce the public good at a cost, or defectors, who can benefit from the public good but do not produce it. We place individuals in a 75×75 spatial grid, with each square being larger than a single individual. Multiple individuals can exist in a square. Thus, while space is discrete, it is not restricted like lattice models where only one individual can occupy a square or node, and instead resembles continuous space in that local densities have no upper limit.

Each individual begins with a random health state, orientation, and memory of previous local density within its own square. At each simulation time step, an individual can divide, produce and consume public good, or die, all probabilistically depending on its health state. An individual moves in either its current orientation or tumbles randomly onto an adjacent square with probabilities that depend on its memory of the previous local density and on the current local density, so as to emulate chemotaxis. The public good diffuses into all four adjacent squares at rates that depend on the individual density of those squares, and is lost to the environment through leaching, which is also mediated by the individual density. Note that even though the public good and individuals can only move to adjacent squares at each time step, they do so at different rates. A list of parameter values is shown in Table A1. The simulation time step is much shorter than that of an average individual generation (~50 time steps), thus approximates continuous time dynamics.

Local densities and clustering coefficients are measured as defined in the main text, using the interaction kernel 2 (Fig. 1).

Appendix B. Spatial game derivation

To obtain a simple spatial game formulation, we begin with a spatial version of the Lotka–Volterra equation (Lotka, 1925; Volterra, 1926).

$$\frac{dX_i}{X_i dt} = r_i + \sum_{j=1}^{2} a_{ij} X_{ij} \tag{B.1}$$

This is clearly a case of the local interaction model with average local densities on the right hand side associated with the linear payoff function coefficient a_{ij}. This equation can be transformed into a frequency-based equation by differentiating X_i/X with respect to time:

$$\frac{dp_i}{dt} = \frac{d}{dt}\left(\frac{X_i}{X}\right) = \frac{dX_i/dt}{X} - \frac{X_i\, dX/dt}{X^2} \tag{B.2}$$

Using Eq. (B.1) as the expression for change in density, Eq. (B.2) becomes:

$$\frac{dp_i}{dt} = \frac{X_i}{X}\left(r_i + \sum_{j=1}^{2} a_{ij} X_{ij}\right) - \frac{X_i}{X^2} \sum_{k=1}^{2} X_k \left(r_k + \sum_{l=1}^{2} a_{kl} X_{kl}\right) \tag{B.3}$$

By replacing density with frequency terms, we finally arrive at:

$$\frac{dp_i}{dt} = p_i\left(r_i + \sum_{j=1}^{2} XC_{ij} a_{ij} p_j - \sum_{k=1}^{2} p_k\left(r_k + \sum_{l=1}^{2} XC_{kl} a_{kl} p_l\right)\right) \tag{B.4}$$

The linear payoff function coefficient a_{ij} is multiplied by the clustering coefficient C_{ij}. To convert Eq. (B.4) into a non-spatial formulation, one only needs to set $C_{ij} = 1$. The result can be readily recognized as the evolutionary game replicator equation (Taylor and Jonker, 1978). This is a slightly different and more straightforward translation between ecological (density-tracking) and evolutionary (frequency-tracking) dynamics than what is already published (Hofbauer, 1981). Since our game formulation is derived from a case of the local interaction model, we conclude that payoffs a_{ij} in game theory are the coefficients of linear payoff functions in the local

Table A1
Simulation parameters and values.

Parameter	Value	Parameter	Value
Background mortality	0.0003	Quorum sensing: rate of exponential decrease in movement probability per individual over quorum	0.2
Maximum health-dependent mortality rate	0.0035	Minimum health to produce public good	0.015
Metabolic cost	1e−6	Maximum public good production	0.005
Minimum health for division at capacity	0.7	Cost to produce maximum dose of public good	0.0005
Maximum division probability	0.075	Public good acquisition rate	0.0025
Carrying capacity within square	20	Rate of conversion from public good to health	5
Quorum: local density above which movement rate decreases exponentially	9	Public good saturation level	1
Minimum health for moving	0.1	Maximum public good horizontal diffusion rate	0.1
Maximum movement probability	0.075	Amount of public good leaching	0.001
Movement cost	0.002	Rate of exponential decrease in public good diffusion due to individual density	0.1
Tumbling probability under positive individual density gradient	0.25		

interaction model. Furthermore, since the clustering coefficients are only constant multipliers of the original payoff terms, the spatial game will follow evolutionary dynamics that is equivalent to the non-spatial game (specified by the replicator equation) with the payoff terms $C_{ij}a_{ij}$.

Appendix C. Games on graphs

Games on saturated static graphs has been an area of intense study recently. Major results from this body of work has been summarized in Tarnita et al. (2009) through a graph structure parameter called structure coefficient (σ). Structure coefficient is a function of number of nodes (individuals), degree (number of links between individuals), other topological attributes of how individuals are arranged, and update rules. The nodes themselves do not move, but they influence the state of linked nodes.

The appropriate selection condition for such a game in the limits of low mutation rate and weak selection is that the fixation probability of morph 1 must be greater than that of morph 2 (Tarnita et al., 2009). The condition states that the morph 1 frequency should be, on average, more than $\frac{1}{2}$. Equivalently, we can ask whether the change in morph 1 frequency (Eq. (B.4)) is greater than zero when the morph 1 frequency is $\frac{1}{2}$ (or $X_1 = X_2$). We readily obtain

$$a_{11}X_{11} + a_{12}X_{12} > a_{21}X_{21} + a_{22}X_{22} \tag{C.1}$$

When morph 1 frequency is $\frac{1}{2}$, we have $X_{12} = X_{21}$ (since $X_1X_{12} = X_2X_{21}$ by conservation of total number of intramorph interactions, and $X_1 = X_2$). So we can divide both sides of the above equation by X_{12} to isolate a_{12} and a_{21}. Further, in a saturated habitat, every individual always has the same number of neighbours, $X_{11} + X_{12} = X_{21} + X_{22} = X$, so $X_{11} = X_{22}$. Eq. (C.1) then becomes:

$$\sigma a_{11} + a_{12} > a_{21} + \sigma a_{22} \tag{C.2}$$

where $\sigma = X_{ii}/X_{ij}$ for any $i \neq j$ when $X_1 = X_2$. At the same time, since $X_{11} = X_{22}$ due to habitat saturation, we recover the implicit restriction that $C_{11} = C_{22}$ for such a game. Thus, $\sigma = C_{ii}/C_{ij}$ for any $i \neq j$ when $X_1 = X_2$. Eq. (C.2) is the same as the result of Tarnita et al. (2009). In another word, structure coefficient is the ratio of intramorph over intermorph average local densities, or equivalently, the ratio of intramorph over intermorph clustering coefficients.

Appendix D. Complex spatial game

We demonstrate how lattice/graph models of spatial game, as exemplified by Van Baalen and Rand (1998) spatial game model of cooperation is a subset of the local interaction model. Pair densities in lattice/graph models are the discrete analogues of average local densities. In particular, the interaction kernel of a lattice/graph model is determined by unweighted links between nodes that can either be occupied by an individual or is empty (but can also be influenced by update rules, as noted by Grafen and Archetti (2008) and Tarnita et al. (2009)). We use the symbol X_{ij} for both pair density and average local density.

The changes in local densities can be tracked using pair approximation (Matsuda et al., 1992), analogous to the moment approximation in continuous space (Bolker and Pacala, 1997). Knowing that morph 1 is the cooperator and morph 2 is the defector (Eq. (D.1)) (adapted from Van Baalen and Rand, 1998) expresses the change in frequency of morph i as a function of the average local densities (or pair densities) X_{i1}, X_{i0} (local density of empty space around morph i) and the structural parameter Y (number of possible spaces around each node). For every available neighbouring empty site, β is a basic intrinsic growth rate that manifests, $b_{i\rightarrow\bullet}$ is the fitness benefit that a morph i individual gives to each present neighbour, and c_i is the cost of being morph i.

$$\frac{dp_i}{dt} = p_i\left(r_i + \left(\beta + b_{i\rightarrow\bullet}\frac{X_{i1}}{Y} - c_i\right)X_{i0}\right) \tag{D.1}$$

This frequency-tracking equation can be converted to a density-tracking equation (by writing $p_i = X_i/X$, and $X_{i0} = Y - X_{i1} - X_{i2}$) and then rearranged by local density terms to reveal the payoff parameters:

$$\begin{aligned}\frac{dX_i}{X_i\,dt} &= r_i + Y(\beta - c_i)\\ &\quad + (b_{1\rightarrow\bullet} - (\beta - c_i))X_{i1} - (\beta - c_i)X_{i2} - \frac{b_{1\rightarrow\bullet}}{Y}X_{i1}X_{i2} - \frac{b_{1\rightarrow\bullet}}{Y}X_{i1}^2\end{aligned} \tag{D.2}$$

We see that the intrinsic growth rate is actually not r_i alone, as the original model suggested, but $r_i + Y(\beta - c_i)$—i.e. there is an intrinsic cost to being morph 1. The payoff is also nonlinear (quadratic), as there are terms associated with X_{i1}^2 and $X_{i1}X_{i2}$; and asymmetric, as the term c_i appears in the local density dependent terms, making the payoff function morph-dependent.

Appendix E. Structured deme model

According to Wilson (1977), individuals interact with equal probability within local trait groups to which their fitness mostly responds, but their maximal movement range at some point in their life cycle defines a deme. Assuming that the deme is saturated, the composition of trait groups that are more fit (produce more progenies) take up more of the deme over time. The fitness of a group is determined by its composition, or proportion of cooperator (say morph 1) versus defector (morph 2). Wilson (1977) showed that if there is between-group variance in their composition, the change in morph density is a function not of morph frequency in a deme, but of "subjective morph frequency". This is the global frequency plus some function of the between-group variance σ^2. In trait groups where undirected helping is proportional to the number of cooperators within group, the dynamic equations, which we have converted from a change in frequency to a change in density form, are (from Wilson, 1977):

$$\frac{dX_1}{X_1\ dt} = b_{1\to\bullet}\left(N_d\left(p_1+\frac{\sigma^2}{p_1}\right)-1\right)-c_1$$
$$\frac{dX_2}{X_2\ dt} = b_{1\to\bullet}N_d\left(p_1-\frac{\sigma^2}{p_2}\right) \tag{E.1}$$

$b_{i\to\bullet}$ is the fitness benefit that a morph i individual gives to each present neighbour, N_d is the group size, $-c_1$ is the intrinsic growth of morph 1, and p_i is the global frequency of morph i. Within group, it is assumed *a priori* there is no assortment, so without between-group variance, we can see that morph 1 (cooperators) density will grow slower than that of morph 2, even if there is a net increase for both morphs due to cooperators helping. In another word, within-group, cooperators are selected against, even though they enhance the absolute fitness of everyone in the group.

If we take $b_{i\to\bullet}$ to be the linear payoff function to average local densities in Eq. (E.1), as is custom in the local interaction model, the average local densities are:

$$X_{ii} = N_d\left(p_i+\frac{\sigma^2}{p_i}\right)-1$$
$$X_{ij} = N_d\left(p_j-\frac{\sigma^2}{p_i}\right) \tag{E.2}$$

X_{ij} is understood as the average number of morph j individuals around a morph i individual, with the interaction kernel being uniform within the range of a trait group and zero everywhere else. From Eq. (E.2), we can solve for the spatial variance:

$$\sigma^2 = \frac{X_i((X_{ii}+1)-X_i)}{N_d^2} = \frac{X_i(X_j-X_{ij})}{N_d^2} \tag{E.3}$$

As may be expected, the spatial variance is inversely proportional to group size squared and proportional to the difference within group between the actual number of ij pairs (X_iX_{ij}) and number of ij pairs expected in the non-spatial scenario ($X_i\ X_j$).

Appendix F. Contextual analysis

Contextual analysis (Heisler and Damuth, 1987) postulates that individual fitness can be written as follows:

$$w_u = \beta_z z_u + \beta_Z Z_u \tag{F.1}$$

where β_z is the selection coefficient for the individual character, β_Z is the selection coefficient for the higher level character, and Z_u is the higher level character that the individual experiences. Then, by plugging Eq. (F.1) into Eq. (4), we obtain:

$$\frac{dz}{dt} = \beta_z var(z_u) + \beta_Z cov(Z_u, z_u) \tag{F.2}$$

where the first term in the right hand side is the individual level selection, and the second term is the higher level selection. The most familiar form of var(z_u) is the genetic variance in a population, for the case where the individual u refers to a gene. An example of cov(Z_u,z_u) is the association between a particular gene variation (allele) and the type of group that the allele finds itself in (whether the group contains more of its own morph or of other morphs).

More generally, we can use Eq. (7) as a basis to analyse levels of selection for a more complicated payoff function Eq. (5). The first two terms in Eq. (7) are straightforward to analyse—with the first belonging to individual-level selection, and the second belonging to higher-level selection. On the other hand, the third term (Eq. (F.3)), referring to payoff function asymmetry, does not neatly fit into one level of selection.

$$(a_{11}-a_{21})cov(z_u x_{u1}, z_u) \tag{F.3}$$

We can break down the covariance term as follows:

$$\begin{aligned} cov(z_u x_{u1}, z_u) &= E\left[z_u^2 x_{u1}\right] - zE[z_u x_{u1}] \\ &= cov\left(x_{u1}, z_u^2\right) + E\left[z_u^2\right]X_{\bullet 1} - z(cov(x_{u1}, z_u) + z\,X_{\bullet 1}) \\ &= X_{\bullet 1} var(z_u) + cov\left(x_{u1}, z_u^2\right) - zcov(x_{u1}, z_u) \end{aligned} \tag{F.4}$$

Note that $X_{\bullet 1}$ is the average local density of morph 1 around any individual. Since $z_u^2 = z_u$ (z_u is either 1 or 0 for each individual), the above equation simplifies to:

$$X_{\bullet 1} var(z_u) + (1-z)cov(x_{u1}, z_u) \tag{F.5}$$

Thus, payoff function asymmetry (a_{11}–a_{21}) contributes to both individual level selection (associated with var(z_u)) and higher-level selection (associated with cov(x_{u1},z_u)).

Appendix G. Inclusive fitness derivation

A one-locus population genetics model that accounts for interaction effects is constructed as follows. The fitness of an individual u is the sum of its intrinsic growth rate, benefits received from each of all other individuals $v(b_{v\to u})$ and all costs exerted upon encounter with v (the plastic cost c_{uv}):

$$w_u = r_u + \sum_{v\neq u}(b_{v\to u} - c_{uv}) \tag{G.1}$$

The changes in the number of morph i individuals (N_i) and of all individuals (N) at a given time are:

$$\frac{dN_i}{dt} = \sum_{u=1}^{N} z_u w_u, \quad \frac{dN}{dt} = \sum_{u=1}^{N} w_u \tag{G.2}$$

z_u is the character value of individual u (where we assign $z_u = 1$ for individuals u belonging to morph i). For instance, if we want to track the change in morph 1 frequency, we can assign morph 1 the character value of 1, and morph 2 the character value of 0. The change in the morph i frequency p_i is then:

$$\frac{dp_i}{dt} = \frac{d}{dt}\left(\frac{N_i}{N}\right) = \frac{dN_i/dt}{N} - \frac{N_i\ dN/dt}{N^2} \tag{G.3}$$

Putting these all together, we obtain:

$$\begin{aligned} \frac{dp_i}{dt} &= \frac{1}{N}\sum_{u=1}^{N}\left(z_u\left(r_u + \sum_{v\neq u}(b_{v\to u} - c_{uv})\right)\right) \\ &\quad - p_i\frac{1}{N}\sum_{u=1}^{N}\left(r_u + \sum_{v\neq u}(b_{v\to u} - c_{uv})\right) \\ &= \frac{1}{N}\sum_{u=1}^{N}(z_u - p_i)\left(r_u + \sum_{v\neq u}(b_{v\to u} - c_{uv})\right) \end{aligned} \tag{G.4}$$

The population structure of this formulation can be understood as being defined for all interacting partners exhaustively (embedded in the summations); similarly, the payoff function to that structure is tallied on an individual basis. In a population with N individuals, there will be N intrinsic growth terms, and $N(N–1)$ cost and benefit terms.

To get to an inclusive fitness formulation, we switch the index of the benefit term between pairs from $b_{v\to u}$ (benefit from neighbour v to focal individual u) to $b_{u\to v}$ (benefit from focal individual u to neighbour v).

$$\frac{dp_i}{dt} = \frac{1}{N}\left(\sum_{u=1}^{N}(z_u - p_i)\left(r_u - \sum_{v\neq u} c_{uv}\right)\right.$$

$$+\sum_{u=1}^{N}(z_u-p_i)\sum_{v\neq u}\left(\frac{z_v-p_i}{z_u-p_i}b_{u\to v}\right)\Bigg)$$

$$=\frac{1}{N}\left(\sum_{u=1}^{N}(z_u-p_i)\left(r_u+\sum_{v\neq u}\left(\frac{z_v-p_i}{z_u-p_i}b_{u\to v}-c_{uv}\right)\right)\right) \tag{G.5}$$

The term $(z_v–p_i)/(z_u–p_i)$ is a correlation coefficient called relatedness, defined for every pair of individuals. The result is similar to that of Grafen (2006).

We must reduce the number of terms for a tractable inclusive fitness model that is comparable to the local interaction model. For a 2-morph population, we associate cost, benefit, and relatedness terms with morph, such that the indices now refer to the morph instead of the individual. We now assume that all individuals of a morph provide the same fitness effect ($b_{i\to\bullet}$) to each interacting neighbour without discrimination. As well, we assume no plastic cost. Then, from Eq. (G.5) we get:

$$\frac{dp}{dt}=\frac{1}{N}\left(\sum^{N_1}(1-p)(r_1+X_{1\bullet}R_1b_{1\to\bullet})\right)+\frac{1}{N}\left(\sum^{N_2}(0-p)(r_2+X_{2\bullet}R_2b_{2\to\bullet})\right)$$

$$=p(1-p)(r_1+R_1X_{1\bullet}b_{1\to\bullet}-r_2-R_2X_{2\bullet}b_{2\to\bullet}) \tag{G.6}$$

where the relatedness terms are:

$$R_1=\frac{X_{11}/X_{1\bullet}-p}{1-p},\quad R_2=\frac{X_{21}/X_{2\bullet}-p}{-p} \tag{G.7}$$

The $\Sigma_{v\neq u}\ldots$ summations from Eq. (G.5) are replaced in Eq. (G.6) by $X_{i\bullet}$ (average total local density around morph i) because both represent the average sum of effects on neighbours by one individual. $(1/N)\Sigma^{Ni}\ldots$ is replaced by p_i times the average of the term in the summation.

Alternatively, we can retain the possibility of helping with discrimination and plastic cost in Eq. (G.5). We obtain:

$$\frac{dp}{dt}=p(1-p)\begin{pmatrix}r_1+X_{11}(R_{11}b_{1\to1}-c_{11})+X_{12}(R_{12}b_{1\to2}-c_{12})\\-r_2-X_{21}(R_{21}b_{2\to1}-c_{21})-X_{22}(R_{22}b_{2\to2}-c_{22})\end{pmatrix} \tag{G.8}$$

By modelling discriminated helping explicitly, we know exactly the relatedness terms *a priori*:

$$R_{11}=1,\quad R_{i12}=\frac{-p_1}{1-p_1},\quad R_{21}=\frac{1-p_1}{-p_1},\quad R_{22}=1 \tag{G.9}$$

We can further simplify the expression of Eq. (G.8) by plugging in Eq. (G.9). We also use the fact that $pX_{12}=(1-p)X_{21}$ by conservation of total number of inter-morph interactions to obtain:

$$\frac{dp}{dt}=p(1-p)\begin{pmatrix}r_1+X_{11}(b_{1\to1}-c_{11})+X_{12}(b_{2\to1}-c_{12})\\-r_2-X_{21}(b_{1\to2}-c_{21})-X_{22}(b_{2\to2}-c_{22})\end{pmatrix} \tag{G.10}$$

With some simple derivation steps, one can see this expression is identical to the spatial Lotka–Volterra Eq. (B.1) and the spatial game Eq. (B.4), both of which are cases of the local interaction model. The following relationship connects the inclusive fitness derivation with the other formulations:

$$b_{j\to i}-c_{ij}=a_{ij} \tag{G.11}$$

Appendix H. *F* statistics

Relatedness has been linked to Wright's *F* statistics, which is the ratio of gene correlation within groups with respect to genes between groups, with group usually meaning a spatial area, as in a deme (Rousset, 2004):

$$F_{st}=\frac{Q_w-Q_b}{1-Q_b} \tag{H.1}$$

Q_w is the probability of identity by morph within groups, whereas Q_b is the probability of identity by morph between random groups. Probabilities of identity are also known as pair densities when they are not conditional on the individuals' morphs (Débarre et al., 2014). These probabilities can be written in term of local densities as

$$Q_w=pE[x_{11}/x_{1\bullet}]+(1-p)E[x_{22}/x_{2\bullet}]$$

$$Q_b=p^2+(1-p)^2 \tag{H.2}$$

In Wright's island model (Lehmann and Rousset, 2010; Rousset and Billiard, 2000), the probability of fixation of cooperation is determined by F_{ST} in place of relatedness. This hinges on the assumption of weak selection, such that we only have to consider the change in frequency near $p=1/2$.

If we assume habitat saturation in all groups, then the local density of any morph-pair cannot exceed X, and the clustering coefficients $C_{11}=C_{22}=C$, leading to the following:

$$E[x_{11}/x_{1\bullet}]=X_{11}/X=Cp$$

$$E[x_{22}/x_{2\bullet}]=X_{22}/X=C(1-p) \tag{H.3}$$

where necessarily Cp is less than or equal to 1. This implies that C cannot be a constant in such a spatially constrained population. In a population where individuals are sparsely distributed across their habitat, it is possible that C stays near constant through all states. Alternatively we can take C to be the within-morph clustering during invasion or at co-existence equilibrium – depending on whether we want to ask about the invasibility or the stability of a phenotype.

Using Eqs. (H.1), (H.2) and (H.3), we obtain the relationship between F_{ST} and C:

$$F_{ST}=\frac{(C-1)Q_b}{1-Q_b}=\frac{(C-1)((1/2p)-1+p)}{1-p} \tag{H.4}$$

Note that the relatedness term R_1 can now be written as

$$R_2=\frac{(C-1)\,p}{1-p} \tag{H.5}$$

We observe that F_{ST} and R_1 only take on the same value when $p=\frac{1}{2}$, which is expected when selection is weak. Precisely, this is when Q_b equals p.

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