ASSORTMENT IN SPACE AND TIME: A FRAMEWORK FOR THE EVOLUTION OF COOPERATION AND MOVEMENT

Short title: Assortment in Space and Time

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ABSTRACT

Despite a proliferation of theories and models of the evolution of cooperation, there is little consensus about the mechanisms that are most important to the selection and maintenance of cooperative behavior. The seeming paradox of the evolution of cooperative behavior is less puzzling when a focus is placed on the role of assortment. The major goals of this paper are to 1) describe a novel framework for understanding the evolution of cooperation based on assortment in space and time, introducing the notion of temporal assortment 2) articulate the general importance of distinguishing passive and active assortment in the evolution of cooperation, and 3) describe why contingent movement in particular is likely to have played an underappreciated role in the evolution of cooperation. This paper proposes a 2x2 framework distinguishing passive/active assortment and temporal/spatial assortment of gene copies, providing a framework for comparing existing models of the evolution of cooperation. Further, this approach suggests connections between areas of research in biology and fruitful new directions for research on the evolution of social behavior.

ASSORTMENT IN SPACE AND TIME

INTRODUCTION

Traditionally, debates about the mechanisms underlying the evolution of cooperation have focused on the relative importance of kin-selection, multilevel selection, reciprocity and complex cognitive/behavioral strategies. Considering the controversy that tends to surround theories about the evolution of cooperation, it is relatively surprising that assortment plays a recognized role in the operation of a wide variety of these proposed mechanisms. Assortment is a way of conceptualizing the proximity of individuals (or genes) of the same type within groups of interacting individuals. Positive assortment, or simply assortment, is the aggregation of the same type within groups, while negative assortment is characterized by less similarity within groups than in the general population.

Kin selection (e.g., Hamilton, 1964a, b), group or multilevel selection (Maynard Smith, 1964; Price, 1970; Wilson, 1987), reciprocity (Axelrod, 1984; Axelrod and Hamilton, 1981; Trivers, 1971) and selection in structured populations such as those on lattices (e.g., Brauchli et al., 1999; Ifti et al., 2004; Nakamaru, 2006; Nowak and May, 1992) or graphs (e.g., Lehmann et al., 2007; Ohtsuki et al., 2006; Taylor et al., 2007) all operate on assortment. This section provides an overview of such theories of the evolution of cooperation, noting that assortment is a fundamentally important aspect of the evolution of cooperation within these divergent approaches.

Models of the evolution of cooperation draw on the formal tools of game theory (von Neumann and Morgenstern, 1944), typically making use of social dilemma (Dawes, 1980) paradigms. Social dilemmas are characterized by a conflict between the individually optimal decision (to defect) and the collectively optimal decision (to cooperate). Because of this conflict between the individually and collectively optimal behaviors, social dilemmas are excellent formal tools for exploring the evolution of social behavior, capturing the tension in benefit optimization at different levels of organization. In dyadic models of cooperation, the prisoner's dilemma and the hawks/doves (also called the snowdrift game) are common (see Doebeli et al., 2005 for a review). Group based interactions are often modeled after public goods games (Ledyard, 1995) and the 'tragedy of the commons' (Hardin, 1968).

Explaining the evolution of cooperative behavior has been a long-term goal in theoretical evolutionary biology. Early field work on the evolution of cooperation focused on behaviors thought to be group and species level adaptations (Wynne-Edwards, 1962; Wynne-Edwards, 1963). Formals models of the evolution of cooperation soon challenged this work, and the individual and gene based views which focused on the average fitness of genes (Dawkins, 1976/1989; Maynard Smith and Price, 1973; Maynard-Smith, 1964; Williams, 1966) came to be more widespread and accepted than 'good of the group' approaches. A major component of this was the formalization of the idea of an evolutionarily stable strategy (ESS), a strategy that cannot be invaded by a mutant strategy when individuals randomly encounter others in an infinite population (Maynard Smith and Price, 1973).

It was, however, recognized that interactions are often not random in the natural world because of limited dispersal of offspring and local interactions, which give rise to interactions with kin. This is captured in inclusive fitness and kin selection models, where individuals preferentially assort with and cooperate with kin, allowing cooperation to evolve (Hamilton, 1964a, b; Maynard Smith, 1964). The fundamental mechanism underlying the operation of kin selection is the selection of genes for a trait (cooperativeness) because of the positive effects the trait has on individuals that share the gene through common descent. The well known equation describing this effect is called "Hamilton's Rule," $c < b*r$; it specifies the cost (c) to benefit (b) ratio required for altruism to evolve between individuals of varying degrees of relatedness (r).

Multilevel/group selection has had a more controversial history (see Sober and Wilson, 1998; Wilson, 1983; Wilson and Wilson, 2007). However, the fundamental features of multilevel selection are the same as those of kin selection: they involve the selection of genes for cooperative traits because of positive effects on others that share (genes that code for) those traits (Maynard Smith, 1964; Price, 1970; Wilson, 1987; Wilson and Wilson, 2007). The mathematics underlying group selection involve measuring the within vs. between group variance in a trait through the variance ratio or another index of assortment (e.g., Pepper, 2000). When there is variation between groups in cooperativeness of the members, the groups with a higher proportion of cooperators are more successful, at least transiently. It has been shown that kin selection can be conceptualized as special case of multilevel/group selection where ‘groups’ are made up of interacting kin (Queller, 1992).

The role of reciprocity in the evolution of cooperation has been the focus of much theoretical and empirical work (Axelrod, 1984; Axelrod and Hamilton, 1981; Bowles and Gintis, 2004; Boyd and Richerson, 1988; Fehr et al., 2002; Gintis, 2000; Nowak and Sigmund, 1998a, b; Panchanathan and Boyd, 2003; Panchanathan and Boyd, 2004; Trivers, 1971). Reciprocity promotes cooperation through long-term benefits to the individual from mutually cooperative repeated interactions. These cooperative interactions are possible without great risk to either partner if they each follow a reciprocal Tit-for-Tat strategy that copies the behavior of their partner on the last round (Axelrod, 1984; Axelrod and Hamilton, 1981). A Tit-for-Tat strategy allows individuals to cooperate when interacting with cooperators and to switch to defection if they encounter defectors, protecting Tit-for-Tat from exploitation, while simultaneously allowing for benefits from repeated interactions with cooperators. This ability to use past behavior as a signal of likely future behavior results in higher long-term payoffs for cooperators compared to defectors.

A variety of more complex and information intensive strategies have been implicated in the evolution of cooperation. For example, relatively recent work has investigated the role of memory (Aktipis, 2006; Cox et al., 1999; deVos and Zeggelink, 1994; Mealy, 1996; Milinski and Wedekind, 1998), reputation (Milinski et al., 2002), gossip (Nakamaru and Kawata, 2002), indirect reciprocity (Nowak and Sigmund, 1998a, b; Panchanathan and Boyd, 2003; Panchanathan and Boyd, 2004), commitment (Nesse, 2001), norm following (Fehr and Fischbacher, 2004; Fehr et al., 2002), policing/punishment (Brandt et al., 2006; Fowler, 2005; Gardner and Westt, 2004) and tag-based cooperation (Hammond and Axelrod, 2006; Spector and Klein, 2006) as possible mechanisms enabling the evolution of cooperation, particularly in humans. Like reciprocity, each of these strategies increases the viability of cooperation through some form of signal processing that decreases uncertainty about a potential partner’s behavioral characteristics, allowing for an adaptive facultative response to that information.

Another area that has received attention is that of partner choice, or exit from interaction. Partner choice has been shown to be a potentially important influence on cooperation in humans (Barclay and Willer, 2007; Boone and Macy, 1999; Orbell et al., 1984; Schuessler, 1989) and various models of partner choice have demonstrated the important role that partner choice can play in the evolution of cooperation (Aktipis, 2004; Ashlock et al., 1996; Connor, 1992; Cox et al., 1999; Enquist and Leimar, 1993; Eshel and Cavalli-Sforza, 1982; Hamilton and Taborsky, 2005; Noe and Hammerstein, 1994; Vanberg and Congleton, 1992). As a result of this individual level partner choice behavior, assortment is promoted and partnerships/groups with more cooperators can end up being more stable and producing more offspring, leading to greater success for cooperators.

PREVIOUS FRAMEWORKS FOR COOPERATION

Each of the approaches described above has contributed importantly to our understanding of the evolution of cooperation. However, confusion arises when kin selection, group selection, reciprocity, partner choice, byproduct benefits and/or direct benefits are conceptualized as alternative categories in which to place instantiations of evolved cooperation. These different approaches rely on the same fundamental principle: that genes having positive effects on copies of themselves will be selected. When individuals with shared genes preferentially assort with one another, this can promote cooperation. In fact, the inclusive fitness framework was developed as a more general approach focusing on positive regression of genotype rather than kinship per se (Hamilton, 1970, 1972). An under-appreciated source of positive regression of genotype (assortment) is that which can arise from the systematic interaction of individuals of different types with their local environments (Hamilton, 1975; Pepper and Smuts, 1999; Pepper and Smuts, 2002; Wilson, 1977).

This general principle (that genes positively affecting copies of themselves will be selected) is difficult to ascertain when looking at recently proposed frameworks for categorizing the evolution of cooperation (e.g., Lehmann and Keller, 2006; Nowak, 2006; Sachs et al., 2004). One of the attractions of previous approaches such as these is that they categorize types of cooperation based on units that are intuitively delineable, such as kin (in kin selection), group members (in group selection), long-term partners (in reciprocity), nearby individuals (in byproducts) and the future self (in direct benefits). However, the intuitive appeal of such classification systems comes at the expense of weak underlying conceptual structure. Proposed classification systems have included four or more primary categories (Lehmann and Keller, 2006; Nowak, 2006), or seven secondary categories (Sachs et al., 2004) that bear little or no systematic relation with other categories within the same classification system. Yet another approach proposed four binary questions that result in sixteen types of cooperation (Bergmuller et al., 2007a). There is a clear need for a succinct and well structured framework in which to understand the evolution of cooperation. I argue here that the concept of assortment in space and time provides such a framework.

Another difficulty with existing frameworks for the evolution of cooperation is that they often collapse evolutionary outcomes with individual level outcomes and individual behavior. Kin selection and group/multilevel selection are evolutionary processes that can change the frequency of cooperative genes in the population given the proper spatial and temporal structure. Direct benefits, indirect benefits and byproduct benefits are ways of describing the individual level outcomes of cooperative interactions between and among individuals. Reciprocity (and other strategies involving information processing) are instantiations of individual level decision rules. Existing classification systems collapse these aspects, making more opaque the distinctions among mechanisms that promote selection for cooperation (those relying on the spatial and temporal structure of the population), the mechanisms that instantiate cooperation (the transmission of benefits) and mechanisms that enable conditional behavior (such as reciprocity). A classification system that respects these distinctions can be a valuable conceptual tool.

The framework proposed in this paper preserves distinctions between evolutionary and behavioral mechanisms within a succinct classification system based on types of assortment. Assortment is a natural choice as a unifying principle around which to understand the evolution cooperation. There is little disagreement about the importance of spatial assortment in the evolution of cooperation. Mechanisms that instantiate cooperation often act on assortment or promote assortment.

Previous work has suggested that an important distinction can be drawn between passive assortment, which is based on structural features of the environment, and active assortment, which involves decision making on the part of the organism (Eshel and Cavalli-Sforza, 1982; Taylor and Day, 2004). This distinction between passive and active assortment is central to the classification system presented here. The present system also introduces the concept of temporal assortment, which, along with spatial assortment, completes a framework for understanding the evolution of cooperation and other behaviors that is concise, straightforward and suggests important directions for new work.

This framework describes several pathways to assortment that promote evolution of cooperation, proposing a 2x2 framework that distinguishes passive from active assortment and temporal assortment from spatial assortment of genes (Table 1). This classification system does not emphasize features that have been traditionally seen as central differences in types of altruism, such as the distinction between the provision of benefits to the self, benefits to kin and benefits to others that share genes for reasons other than decent (Lehmann and Keller, 2006; Nowak, 2006; Sachs et al., 2004). Instead, this classification system focuses on the spatial and temporal association of genes with copies of themselves via direct interactions or indirect interactions through a shared environment. Because genes can influence the viability of copies of themselves that are distant in space and/or time, selection should be expected to optimize net benefits to genes over both spatial and temporal tradeoffs.

Other proposed frameworks for the evolution of cooperation (Bergmuller et al., 2007a; Lehmann and Keller, 2006; Nowak, 2006; Sachs et al., 2004) preserve the distinction between effects on others from effects on the self, because it is thought that behaving in a way that benefits the self in the future does not constitute an altruistic or cooperative act. The present classification system does not make any categorical distinction based on the entities that are the recipients of the benefits. Instead, cooperation is conceptualized as any benefit providing act in which there is statistical uncertainty about the benefits and/or costs accruing to copies of the gene in at various spatial and temporal distances. This draws on certain aspects Buston and Balshine (2007) uncertainty approach to conceptualizing acts of cooperation. Because this is an untraditional use of the term ‘cooperation’ the terms ‘benefit emission’ and ‘benefit transmission’ are favored throughout this paper.

TABLE 1

Framework for assortment

ASSORTMENT IN SPACE AND TIME	Passive: Byproduct of ecological/demographic processes	Active: Conditional response to social/ecological signals
Spatial proximity of genes	Passive spatial assortment	Active spatial assortment
Temporal proximity of genes	Passive temporal assortment	Active temporal assortment

Table 1. The present framework is characterized by a 2x2 framework that distinguishes passive/active assortment and temporal/spatial assortment.

TEMPORAL ASSORTMENT

One of the unique contributions of this paper is to introduce the notion of temporal assortment. Central to temporal assortment is the idea that individuals can behave in ways that have long-term effects on their local environments by enriching or depleting their environments. This can influence the viability and fitness of individuals who occupy that same environment during future time periods, even after the individual has died or moved from that particular local environment. This is the essence of temporal assortment and its evolutionary implications: that individuals can have effects on their local environments, and that these effects can carry forward through time to influence the fitness of individuals who occupy that environment in future time periods (including but not limited to the self).

It is suggested here that temporal assortment, along with spatial assortment, form a comprehensive framework for understanding the evolution of cooperation. Recall that spatial assortment is the nonrandom spatial proximity with entities that share genes. Temporal assortment is analogous to this; it is the nonrandom *temporal* proximity of entities that share genes. This temporal proximity can be important to the evolution of cooperation when individuals can have long-lasting effects on their local environments.

The long-term association with the environment (which promotes temporal assortment) can be conceptualized as a 'coupling' with the local environment. The most straightforward form of temporal assortment of genes is the effect that individuals can have on their own payoffs in future time periods as a result of a long-term association with their physical and social environments. In other words, an individual who invests in its local environment is likely to get benefits from that enriched environment in the future. To the extent that highly investing individuals remain coupled with their local environments, they can reap gains from the behavior of their past selves or the past behavior of other individuals (such as parents, other kin or social partners) that invested in the same local environment (or experience costs in the case of previous exploitation of that environment). Environmental feedback resulting from temporal assortment allows for payoffs of an individual to be influenced by the past behavior of itself and others that have occupied that local environment. These long-term effects that result from interactions with a shared environment can make temporal assortment important to the evolution of cooperation.

The importance of such long-term social interactions has been noted in other approaches to the evolution of cooperation. More specifically, temporal assortment is closely connected to the ideas of extended associations and partner fidelity feedback (Axelrod, 1984; Axelrod and Hamilton, 1981; Bull and Rice, 1991; Sachs et al., 2004; Trivers, 1971). However, in the present framework temporal assortment is not conceptualized as necessitating a specific interaction partner. Other classification systems simply conceptualize long-term benefits as 'direct benefits' (Lehmann and Keller, 2006) or 'direct reciprocity' (Nowak, 2006) from other social actors. Again, the temporal assortment category differs in that it captures both interactions with the social environment and interactions with the physical world that can have long-term effects on payoffs for copies of genes.

At the most basic level, temporal assortment is the long-term association of an individual with its local environment. If individuals exploit their local environments, this can result in long-term cost, but if individuals invest in their environments, this can result in long-term benefits. The long term effects on individual investment in a partner has been proposed as an essential factor in the classification of the cooperative interactions in another recent framework (Bergmuller et al., 2007b), but again the present framework includes interactions with the local environment more generally rather than only with a specific interaction partner.

ASSORTMENT IN SPACE AND TIME

In general, extended coupling with the environment will be advantageous for organisms that enrich their local environments, while some amount of decoupling will be advantageous for entities that deplete those environments. The ability of individuals to change their local environments by moving in space can allow individuals to optimize their coupling and decoupling with the environment to maximize their rate of return from the environment, as in optimal foraging models (MacArthur and Pianka, 1966; Stephens and Krebs, 1986). A simpler process is at work in contingent movement models of the evolution of cooperation such as the Walk Away model (Aktipis, 2004; Aktipis, 2008) and models of environmental feedback (Pepper, 2007; Pepper and Smuts, 1999; Pepper and Smuts, 2002). These approaches capitalize on the ability of entities to process information about returns from the environment (i.e., temporal assortment information) and respond to this information by moving. This results in temporal assortment information (the rate of return from coupling with the environment) potentially affecting the spatial assortment of the population. These kinds of interactions between spatial and temporal assortment are discussed in greater depth in later sections.

ASSORTMENT: A COHESIVE FRAMEWORK

In this section I describe in greater depth the four types of assortment that emerge from the 2x2 framework of passive/active and spatial/temporal assortment. This framework is both concise and has an underlying conceptual structure (Table 1), providing an alternative to classification systems that delineate a moderate number of conceptually unrelated categories (Lehmann and Keller, 2006; Nowak, 2006; Sachs et al., 2004), or a very large number of related categories (Bergmuller et al., 2007a).

The categories described below emerge from distinctions between passive/active assortment and spatial/temporal assortment. Passive assortment emerges as a byproduct of ecological and demographic processes. Active assortment, on the other hand, arises from the processing of information in the environment and contingent responses to information. A distinction is also made between processes that rely on temporal assortment of genes and those that rely on spatial assortment of genes. When a gene codes for behaviors that have effects on copies of the gene that are distant in time or space, this can affect selection pressures for cooperative behavior.

Previous frameworks of the evolution of cooperation have collapsed evolutionary outcomes (selection, e.g., ‘kin selection’) individual level effects (benefits, e.g., ‘direct benefits’), and contingent rules (information processing/decision rules, e.g., ‘Tit-for-Tat’). The conceptual intermingling of processes that operate on very different levels has contributed to confusion about the most effective categorical distinctions between different types of cooperation. The present approach (summarized in Table 2) clearly distinguishes between processes operating at each of these levels, describing individual level benefits/costs, evolutionary outcomes and (for active assortment) information processing components for each type of assortment. Note that in the information input row, active temporal assortment uses spatial assortment information while active spatial assortment uses temporal assortment information (this interaction is further described in Figure 2 and the section on feedback between spatial and temporal assortment). The final row of Table 2 lists terms from the literature that can have been used to describe phenomena falling into these categories.

Importantly, diverse theoretical and computational models of the evolution of cooperation can be placed in this framework (Table 3). Each of these models can be conceptualized in terms of passive/active assortment components and temporal/spatial assortment components.

TABLE 2
Characteristics of four types of assortment

	Passive: Byproduct of ecological/demographic processes		Active: Conditional response to social/ecological signals	
	Passive Temporal	Passive Spatial	Active Temporal: Contingent Benefit Transmission	Active Spatial: Contingent Movement
Cost/benefit structure	Future costs/benefits on genes from coupling with environment	Costs/benefits on genes from spatial proximity with copies	Future costs/benefits on genes from coupling with environment	Costs/benefits on genes from spatial proximity with copies

Information input	N/A	N/A	Signals of costs/benefits from spatial assortment	Signals of costs/benefits from temporal assortment
Instantiations	Local benefit production, local resource consumption	Local reproduction, limited dispersal	Kin recognition, tag-based altruism, TFT, reputation/gossip/ indirect reciprocity	Benefit approach, Walk Away, optimal foraging
Social/physical environmental result	Fitness coupled with local physical or social environment	Proximity of kin that share genes	Change in cooperativeness or propensity to enrich or deplete environment	Movement and/or restructuring of physical or social environment
Evolutionary result	Selection for genes that optimally trade-off costs and benefits to all copies of genes in various time periods	Selection for genes that optimally trade-off costs and benefits to all copies genes in nearby individuals	Selection for ability to contingently cooperate to optimize costs and benefits over time	Selection for ability to contingently move or restructure environment to optimize costs and benefits over all copies of genes in different spatial locations
Terms in the literature	*Future benefits, environmental feedback, partner fidelity feedback*	*Indirect benefits, inclusive fitness, non-random matching, kin selection, structural assortment*	*Reciprocity, partner fidelity feedback, kin recognition, Tit-for-Tat*	*Partner choice, exit, selective assortment, Walk Away, environmental feedback*

Table 2. The present classification system distinguishes between passive and active forms of assortment as well as temporal or spatial assortment of gene copies. Basic instantiations of these various types, as well as a description of potential environmental and evolutionary results are provided in this table. The final column notes terms that have been used in the literature to describe mechanisms that fall into these categories, with some overlap of terms.

Passive Assortment

Passive assortment is a way of describing the proximity of genes that emerges from structural features of the social and physical environment. The distinction between passive and active assortment has been made in previous work (Eshel and Cavalli-Sforza, 1982; Taylor and Day, 2004) and is expanded upon here by distinguishing between spatial and temporal processes. Passive assortment results from ecological and demographic processes such as local resource consumption and local investment (in temporal assortment) and local reproduction and dispersal (in the case of spatial assortment).

Passive Temporal Assortment

Passive temporal assortment is the temporal association of genes with copies of themselves as a result of ecological and demographic processes. For example, immobile individuals who consume resources in their local environments negatively affect the resources available to copies of their genes (in themselves and potentially nearby kin) in future time periods. In contrast, individuals that enrich their local environments by producing beneficial products positively affect the resources available to copies of their genes in future time periods. These types of interactions result in a sort of 'fitness coupling' of individuals with their local environments and subsequent selection for optimal tradeoffs between the benefits and costs of depletion/enrichment of the environment over the relevant time frame.

The idea of passive temporal assortment integrates the ideas of future benefits (Axelrod, 1984; Buston and Balshine, 2007; Trivers, 1971), environmental feedback (Pepper, 2007; Pepper and Smuts, 1999; Pepper and Smuts, 2002), and partner fidelity feedback (Bull and Rice, 1991; Sachs et al., 2004) into cohesive framework. In all of these cases, an individual either depletes or enriches its local environment, with long-term consequences. In passive temporal assortment, these long-term consequences emerge simply from demographic and ecological interactions and do not involve the active responses to the environment.

Passive Spatial Assortment

Like passive temporal assortment, passive spatial assortment does not involve the processing of information, resulting simply from structural and demographic processes. In the case of spatial assortment, the most important processes are those underlying local reproduction and limited dispersal (Eshel and Cavalli-Sforza, 1982; Taylor and Day, 2004). When demographic features of the population generate spatial proximity of individuals that are more genetically similar than the overall population, this is passive spatial assortment. Spatial assortment results in selection for genes that optimally tradeoff costs and benefits to all copies of genes in nearby individuals, as, for example, in models of kin selection (Hamilton, 1964a, b), and multilevel selection (Maynard Smith, 1964; Price, 1970; Wilson, 1987).

Passive spatial assortment captures several categories included in previous classification systems of cooperative interactions. Specifically, 'kin fidelity' (Sachs et al., 2004), 'kin selection' (Lehmann and Keller, 2006; Nowak, 2006), and 'indirect benefits' (Bergmuller et al., 2007a) are ways of describing the outcomes of spatial assortment on individuals and evolutionary processes. The present approach focuses on the structural features of the population (spatial proximity with individuals who share genes) as the main feature, and describes the social and evolutionary outcomes separately (see Table 2). This is in contrast to other classification systems which collapse the structural features with the individual level (i.e., indirect benefits) or evolutionary outcomes (i.e., kin selection) of preferential benefit transmission to kin.

Active Assortment

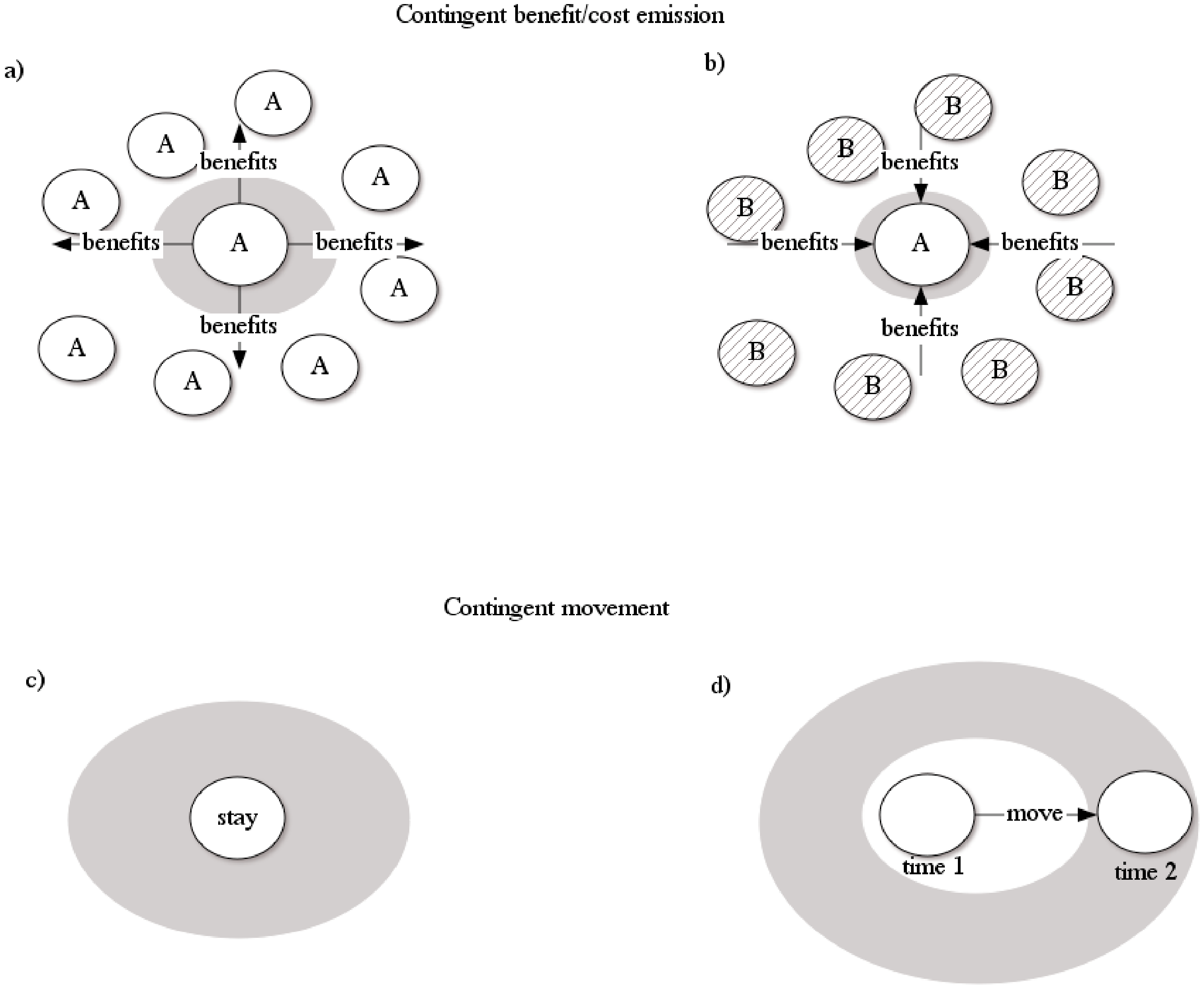
The ability to respond to information in the environment in ways that promote the long terms success of genes is highly adaptive and is the essence of active assortment. Most organisms take in information from the environment and respond contingently, either through changes in gene expression in response to environmental cues or through neural systems that process incoming perceptual inputs. To the extent that the processing of this information can decrease the uncertainty about the costs/benefits from alternative behaviors, it can produce adaptive contingent responses. This leads to the selection of information processing abilities and decision rules that can promote active assortment. The ability to respond contingently enables individuals to engage in behavior that promotes their own survival and reproduction.

Furthermore, contingent behavior creates effects on the social and physical environment that can have important influences on the proximity and viability of copies of genes that are near in space and time. In other words, the ability to respond to information from the environment can lead to changes in assortment. The processing of information from the environment is the essence of active assortment, whether from the social environment (Eshel and Cavalli-Sforza, 1982; Pepper, 2007; Taylor and Day, 2004) or the physical environment (Pepper and Smuts, 1999; Pepper and Smuts, 2002).

Most analytical models take behavioral assortment (or its precursors) as a variable to change parametrically, making it difficult to investigate the role of active assortment in the evolution of cooperation. Classic models of kin selection compute whether an altruistic behavior will be selected using degree of kinship as an independent variable (Hamilton, 1964a, b) and multilevel selection models typically rely on the ratio of between-group variance to within-group variance, which is not assumed to change due to active choice on the part of the individuals within the group (Maynard Smith, 1964). Kinship and the ratio of between to within-group variance are ways of describing spatial assortment.

It is proposed that here that active assortment is guided by two fundamental types of contingent behavior, 1) the conditional transmission of benefits (or costs) which promotes active temporal assortment, and 2) responsive movement or other restructuring of the local environment which promotes active spatial assortment. Both types of contingent behavior take information from the environment and operate on the information with adaptive decision rules.

When individuals process information from the environment and contingently respond to that information, this can create active assortment. In active temporal assortment, individuals respond to information in ways that increase the likely long-term benefits of associations with the (physical or social) environment. Active spatial assortment, on the other hand, involves responding to information in the environment in ways that increase spatial proximity with those who share genes.



Contingent benefit/cost emission

Contingent movement

Figure 1. Active assortment occurs when agents process information from the environment and behave contingently, emitting benefits/cost or moving in response to information from the environment. In this figure, agents of the same or different type are represented by As and Bs and benefits are represented by gray regions. a) If cues of positive spatial assortment are high (indicating that individuals of the same type are likely to be nearby), it can be advantageous to enrich the environment by emitting benefits (large grey circle). b) If spatial assortment is low, it can be more advantageous to deplete the environment and/or refrain from emitting benefits (small grey circle). c) When individuals occupy a rich (physical or social) environment (grey circle), it can be beneficial to stay in that environment as long as the rate of return is high enough. d) If the current environment is sufficiently depleted or uncooperative (empty region in grey circle), moving or otherwise restructuring the environment can provide greater benefits over time.

Active Temporal Assortment: Contingent benefit/cost emission

In active temporal assortment, individuals can respond to information in the environment by depleting or enriching that (physical or social) environment. This can occur at the level of interactions with resources in the physical environment or at the level of social interactions with other individuals. In the case of interactions with the physical environment, individuals might, for example, contingently switch from consuming and enriching the environment based on various cues. In social interactions, individuals might contingently cooperate based on information from the environment.

Many models of the evolution of cooperation and frameworks have explicitly or implicitly addressed the role of contingent benefit transmission. The ideas of reciprocal behavior (Trivers, 1971), Tit-for-Tat (Axelrod, 1984), partner fidelity feedback (Bull and Rice, 1991; Sachs et al., 2004), and some aspects of kin recognition can be grouped into the general category of active temporal assortment, where individuals can benefit from contingently cooperating because of the long-term benefits to genes of continued associations.

Reciprocity is based on the principle of conditional cooperation (Trivers, 1971), and the famous reciprocal Tit-for-Tat strategy (Axelrod, 1984; Axelrod and Hamilton, 1981) is successful because it transmits benefits only to others with a history of past cooperation, i.e., other Tit-for-Tat agents or unconditional cooperators. The PAVLOV strategy (Nowak and Sigmund, 1993) contingently transmits benefits only to others that contingently transmit benefits. Interestingly, PAVLOV occasionally 'tests' its partner by defecting and resumes cooperation only if the partner responded to defection by defecting. This allows PAVLOV to reap the benefits of exploiting agents that do not contingently transmit benefits.

Models of more complex information processing strategies such as those based on reputation, gossip or indirect reciprocity (as reviewed above) involve the contingent transmission of benefits. In these models, individuals transmit benefits only when the partner's known interaction history is sufficiently cooperative. Contingent benefit transmission has been widely explored in models of the evolution of cooperation (see Table 2).

Somewhat paradoxically, the ability to recognize kin can be considered a case of active temporal assortment. In kin recognition, organisms take in spatial assortment information (in the form of cues from the social environment decrease the statistical uncertainty that a prospective partner shares genes), and respond to that in a way that can actively change the benefits available in future time periods for all copies of the genes (i.e., temporal assortment). This pathway from spatial assortment cues to active temporal assortment is laid out at the top of Figure 2. It is well-accepted that spatial assortment can favor the evolution of recognition mechanisms which allow for conditional transmission of benefits towards kin (e.g., via kin selection; Hamilton, 1964a, b), but the present framework suggests a novel framing that includes both temporal assortment in and spatial assortment processes.

Active temporal assortment is based on the ability of individuals to contingently enrich or deplete the physical or social environment in ways that provide long-term benefits to all copies of the genes (Figure 1 a and b). Because different types of physical and social environments can create different temporal cost/benefit profiles for different alternative behaviors, the ability to respond to information from the environment and choose (enrichment or depletion) behaviors based on that information can result in higher overall payoffs.

Active Spatial Assortment: Contingent movement

Few models of the evolution of cooperation have explicitly explored the role of movement in space. Despite great attention to the contingent transmission of benefits, contingent movement in space might be as important of a fundamental principle guiding the evolution of cooperation. Contingent movement not only allows for individual level adaptive responses (leaving areas with insufficient benefits, Figure 1 c and d) but also can cause changes in aggregate dynamics that can influence selection dynamics, ideas that are discussed in greater depth in the section on feedback between spatial and temporal assortment.

Active spatial assortment is at work when individuals process information from the environment by moving or otherwise restructuring the population in a way that tends to lead to non-random spatial proximity of individuals that share genes. For example, movement away from uncooperative partners or groups can lead to the systematic association of cooperators with one another. This is the essence of the Walk Away model (Aktipis, 2004; Aktipis, 2008) and similar models of movement in response to environmental feedback (Pepper, 2007; Pepper and Smuts, 1999; Pepper and Smuts, 2002).

Over evolutionary time, selection will favor individuals who are able to move or restructure their social environments in ways that optimize the costs and benefits to all copies of genes (over space). Despite the fact that preferential interactions with kin have been long considered an important factor in the evolution of cooperation, the importance of active spatial assortment in promoting the evolution has been underappreciated due largely to the non-spatial nature of traditional analytical models.

Responsive movement in space has been modeled in only a few published simulations (Aktipis, 2004; Hamilton and Taborsky, 2005; Pepper, 2007; Pepper and Smuts, 1999; Pepper and Smuts, 2002), despite the apparent importance of spatial proximity in social interactions for most species. However, partner choice models capture the notion of 'leaving' uncooperative partners (Ashlock et al., 1996; Connor, 1992; Cox et al., 1999; Enquist and Leimar, 1993; Eshel and Cavalli-Sforza, 1982; Noe and Hammerstein, 1994; Vanberg and Congleton, 1992) or restructuring the social network so that future interactions to not occur with an uncooperative past partner (Fu et al., 2007; Masuda and Aihara, 2003; Santos et al., 2006). Partner choice and network models such as these have begun to address the importance of the active processing of information in promoting preferential interactions. However, even these models rarely embed individuals in explicit space, leading to the loss of a potentially rich source of embedded ecological information (i.e., the statistical association between spatial proximity and genetic similarity) that can emerge from contingent movement rules.

Agent based models that explicitly model agents in space have demonstrated that when individuals are able to respond to information in the environment in ways that lead to spatial proximity and therefore preferential interactions with those that are likely to share genes, cooperation can be promoted (Aktipis, 2004; Pepper, 2007; Pepper and Smuts, 1999; Pepper and Smuts, 2002). However, the resulting movement can have effects on the spatial structure of the population, influencing spatial assortment in ways that can also have important effects on evolutionary dynamics (Aktipis, 2008). This is the topic of the final section.

TABLE 3

A Framework for Models of the Evolution of Cooperation

	Passive Temporal	Passive Spatial	Active Temporal: Contingent Benefit Transmission	Active Spatial: Contingent Movement
(Hamilton, 1964a, b)		Interactions with kin		
(Maynard Smith, 1964)	Metapopulation	Offspring placed in group, interactions within group, occasional migration		
(Trivers, 1971)	Repeated interactions		Reciprocity	
(Axelrod and Hamilton, 1981)	Repeated interactions		Tit-for-Tat	
(Eshel and Cavalli-Sforza, 1982)	Individuals are more likely to encounter same strategy			Individuals actively choose partners of same type
(Peck and Feldman, 1986)	Repeated cooperative interactions in dyads			
(Wilson, 1987)	Metapopulations	Offspring placed in group, occasional migration		
(Dugatkin and Wilson, 1992)	Metapopulation			Defectors condition interaction on marginal value theorem
(Killingback and Doebeli, 1996; Nowak and May, 1992)	Lattice, neighborhood interactions	Successful strategies repopulate neighbors		
(Vanberg and Congleton, 1992)	Repeated PD encounters			Individuals refuse to play with known defectors
(Enquist and Leimar, 1993)	Repeated cooperative interactions in dyads or groups	Offspring placed in group	Cooperation offered after cooperation is demonstrated	Interaction propensity contingent on reputation
(Nowak and Sigmund, 1993)	Repeated encounters of PD partners		Cooperation contingent on partner's previous behavior	
(Lindgren and Nordahlb, 1994)	Lattice, neighborhood	Successful strategies repopulate neighbors		

	interactions			
(Ferriere and Michod, 1995)	One-dimensional interaction space, local interactions	Offspring placed nearby (but with diffusion approximated mobility)	Cooperation contingent on partner's previous behavior	
(Ferriere and Michod, 1996)	One-dimensional interaction space, local interactions	Offspring placed nearby		
(Ashlock et al., 1996)	Repeated PD interactions			Individuals refuse to interact with insufficiently cooperative partners
(Epstein, 1998)	Lattice, local interactions	Offspring placed on neighboring sites		
(Brauchli et al., 1999)	Lattice		Cooperation contingent on partner's previous behavior	
(Cox et al., 1999)	Repeated encounters of PD partners		Cooperation contingent on partner's previous behavior	Entering interaction contingent on partner's previous behavior
(Mitteldorf and Wilson, 2000)	Lattice, local interactions, some instability of neighborhood	Offspring placed on neighboring sites		
(Avilés, 2002)	Metapopulation, local interactions	Linkage disquilibrium between group joining and cooperation		
(Pepper and Smuts, 2002)	Lattice, local interactions through shared use of renewable resource patches			Individuals leave areas with low resource levels
(Marshall and Rowe, 2003)	Lattice, varied viscosity, local PD interactions	Local reproduction	Memory and Tit-for-Tat	
(Suzuki and Arita, 2003)	One dimensional ring, N-player PD with neighbors	Limited dispersal		
(Aktipis, 2004)	Lattice, local interactions			Individuals move after encountering defectors
(Fletcher and Zwick, 2004)	Metapopulations, public goods interactions			
(Gardner and Westt, 2004)	Metapopulation		Facultative increase in punishment with higher local cooperativeness	
(Ifti et al., 2004)	Lattice, Network	Successful strategies repopulation neighbors		
(Hamilton and Taborsky, 2005)	PD interactions among group members	Interactions within groups but offspring disperse	Individuals condition their cooperation on past outcomes	Individuals leave group conditional on their own strategy and PD outcome
(Fu et al., 2007; Masuda and Aihara,	Network	Successful strategies		Agents rewire

2003; Santos et al., 2006)		repopulate neighbors		network connections
(Ohtsuki et al., 2006; Pacheco and Santos, 2005; Santos and Pacheco, 2006; Santos et al., 2006; Santos et al., 2005)	Network	Successful strategies repopulate neighbors		
(Zhang et al., 2005)	Lattice, local PD interactions	Colonization of nearby patches		
(Hammond and Axelrod, 2006)	Local interactions	Reproduction is local	Behavior is conditional on partner's tag	
(Hauert et al., 2006),	High average payoff (high proportion cooperators) increases the growth rate			
(Killingback et al., 2006)	Metapopulations			
(Spector and Klein, 2006)	One dimensional ring, interaction in varied neighborhood sizes	Local reproduction, limited dispersal	Altruism performed only when tags are similar enough	
(Janssen and Goldstone, 2006)	Metapopulation, local public good interactions	Local reproduction		
(Traulsen and Nowak, 2006)	Metapopulation, within group altruistic interactions	Local reproduction		
(Fletcher and Zwick, 2007)	Metapopulations, public goods interactions			Regrouping occurs at temporal point when proportion of cooperators begins to decrease*
(Ohtsuki and Nowak, 2007)	Network		Direct reciprocity	
(Taylor et al., 2007)	Network	Interacting partners can displace one another upon reproduction		
(Wakano, 2007)	Lattice	Colonization of nearby patches, spatial diffusion of benefits		

Table 3. This table provides a summary of the types of assortment at work in various agent-based, spatial and historically important models of the evolution of cooperation models. Cooperation is promoted through passive temporal, passive spatial, active temporal and/or active spatial assortment.

*In Fletcher and Zwick (2007), the time of regrouping is determined by the decrease in cooperators. In their simulations, agents did not actively process this information, but the timing of the regrouping was determined by the global procedures making use of a contingent rule that took in information from the environment and responded to that information by creating a change in grouping.

FEEDBACK BETWEEN SPATIAL AND TEMPORAL ASSORTMENT

The ability of organisms to respond contingently to information in the environment can lead to interactions between spatial and temporal assortment. As individuals contingently emit benefits and move, they affect the benefit structure (temporal assortment) and social structure (spatial assortment) of the environment, respectively. This individual-level contingent behavior results in the presence of new information about temporal and spatial assortment, which can then be used as input to the contingent rules. These dynamics lead to potentially complex feedback loops wherein the active processing of information about temporal assortment can lead to changes in spatial assortment and vice versa (Figure 2).

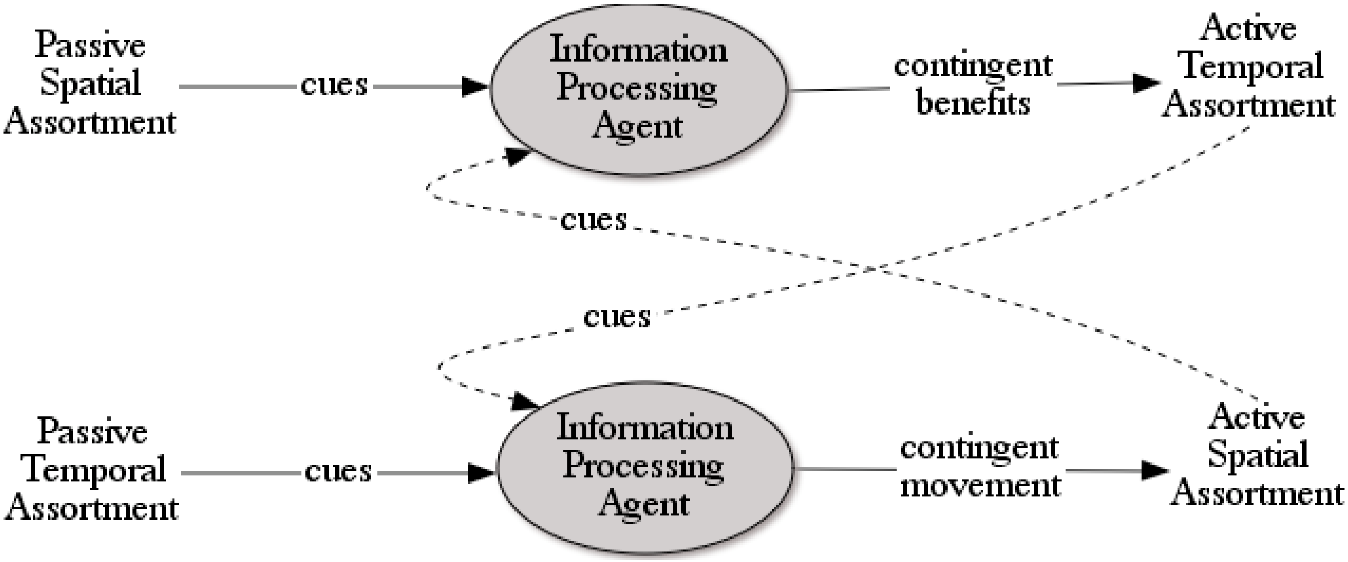


Figure 2. When individuals are able to process information from the environment and respond to that information contingently, feedback loops between temporal and spatial assortment can emerge. Agents can respond to spatial assortment information by contingently transmitting benefits, which can then influence temporal assortment. Likewise, agents can respond to temporal assortment information by moving or restructuring the social environment, which can have important effects on spatial assortment.

Active Temporal Assortment Results from Contingent Responses to Spatial Assortment

Organisms can respond to spatial assortment information in ways that create changes in temporal assortment. When individuals change their propensity to invest in or exploit the environment based information from the environment, this can have long term effects on the benefits available in the environment in future time periods, creating active temporal assortment. As discussed in the section on active temporal assortment, if an individual is able to respond to cues of likely kin proximity (spatial assortment information) by altering cost/benefit emission, this changes the availability of benefits in the environment in future time periods (leading to active temporal assortment). In other words, information about spatial assortment can be used in contingent benefit emission rules, which leads to active temporal assortment. This is schematized in the top part of Figure 2.

Active Spatial Assortment Results from Contingent Responses to Temporal Assortment

Temporal assortment cause changes in the long-term payoffs to individuals based on interactions with the local environment. It has been shown that if individuals can process information from the environment, e.g., by leaving exploited regions, spatial associations of cooperators emerge (Pepper and Smuts, 1999; Pepper and Smuts, 2002). This occurs because exploitative or uncooperative individuals create poor environments, leading to greater instability of regions with such individuals. On the other hand, individuals who refrain from exploiting (or actively enrich) the environment create more stable regions. Because the degradation of the environment contains information about the temporal effects of continued coupling with the local environment, organisms can adaptively respond to that information by moving in space, which can generate a change in spatial assortment. This leads active spatial assortment to emerge from agent’s responses to temporal assortment cues (Figure 2, bottom).

Feedback Between Active Temporal and Spatial Assortment

The presence of entities that can process cues about spatial and temporal assortment and respond to those contingently opens up the possibility for mutual feedback between temporal and spatial assortment (Figure 2, dashed arrows) that would not exist if individuals could not process and respond to information from the environment. Because organisms have decision rules that can operate on temporal and spatial assortment information, organism-generated assortment can feed back into those information processing systems. Active temporal assortment creates information that can enter into processing systems for temporal assortment, and active spatial assortment creates information that meets input conditions for the systems that process spatial assortment. The dynamics that emerge from these interactions are likely to be important in the evolution of cooperation and movement and will be explored in future work.

DISCUSSION

Despite the intuitive attractiveness of drawing categorical distinctions between 'kinds' of cooperation that benefit entities such as kin, group members, long-term partners or the future self, this intuitive ontology has obscured the central importance of the underlying genetic reality: that genes often do not code for behaviors that increase fecundity of themselves directly, instead affecting copies of the genes (Hamilton, 1964a, b; Hamilton, 1975). The framework proposed here suggests that there are two main ways that genes can affect copies of themselves: through spatial and temporal proximity. Models of the evolution of cooperation can be classified according to the roles of spatial and temporal assortment, and the capacity of individuals to behave contingently results in the possibility of active assortment, where information from the environment is processed in ways that can create feedback between spatial and temporal assortment. The distinctions between passive/active assortment and spatial/temporal assortment form the basis for the present framework for classifying models of the evolution of cooperation.

It is a fact of population biology that the evolution of any trait is due to the increase in copies of the gene coding for that behavior in the population. Ceteris paribus, the effect the gene has on the fitness of 'itself' is no more important than the effect on *copies* of itself. This makes assortment a natural choice as a unifying conceptual framework for understanding the evolution of cooperation. The distinction between passive and active assortment is already well-appreciated, as is the importance of spatial assortment (Eshel and Cavalli-Sforza, 1982; Taylor and Day, 2004). The present paper adds the notion of temporal assortment, showing that this allows for a comprehensive conceptual framework that can incorporate previous theoretical and simulation models of the evolution of cooperation.

Many organisms are likely to have evolved the ability to contingently respond to the environment because of the benefits that can be gained from contingent behavior. Movement away from cost producing entities, toward benefit producing entities, and lack of movement when in the presence of entities producing sufficient benefits are likely to be among the first behaviors that evolution acted upon. Extremely simple organisms can use responsive movement to avoid toxins and approach energy-rich regions, suggesting that these rules can be used by organisms without a nervous system, probably through functions executed by regulator regions of the genome.

Selection for simple contingent behaviors can have important effects at the population level, leading to spatial and/or temporal assortment of individuals who emit benefits, and subsequent changes in selection pressures. Contingent benefit transmission is the focal point of many proposed mechanisms promoting the evolution of cooperation including kin recognition, reciprocity and tag-based systems. However, the importance of contingent movement has received comparatively less attention in the literature on the evolution of cooperation.

The present approach also provides a framework that can be of value to zoologists, cell biologists, oncologists, behavioral ecologists, population biologists and even animal cognition and decision making researches. The remainder of this section proposes ways that the proposed conceptual framework might enrich and connect these sub-disciplines.

For example, contingent movement and benefit production are likely to be important in conflict and cooperation between cells. Cooperation between cells has been considered as one of the major factors in evolutionary transitions in individuality (Maynard Smith and Szathmary, 1995; Michod, 1999). Conceptualizing and even measuring cellular-level interactions in terms of spatial and temporal assortment might provide insights into problems such as those underlying the conflict within multicelluar organisms. For example, cancer is characterized by both the transmission of benefits (i.e., blood) to cancer cells and movement of these cells throughout the body (as in metastasis). The importance of movement and cooperation in evolutionary and ecological approaches to cancer has been noted elsewhere (Merlo et al., 2006). The present approach might provide further traction for this approach, suggesting potential roles of temporal and spatial assortment in influencing the evolution and behavior of cancer cells.

Movement in response to environmental features plays an important role in both social and non-social aspects of behavior. In addition to clear connections to the Walk Away model (Aktipis, 2004; Aktipis, 2008) and models of environmental feedback (Pepper, 2007; Pepper and Smuts, 1999; Pepper and Smuts, 2002), these concepts are important in the evolution of behaviors traditionally considered separate from questions about the evolution of cooperation. For example, foraging adaptations are based on rules for evaluating current and future outcomes of staying in the local environment or moving to a new environment (MacArthur and Pianka, 1966; Stephens and Krebs, 1986), potentially promoting spatial assortment through the processing of temporal assortment information. Further, the processes underlying migration between groups, colonization of new environments and invasion of other groups all require movement in space. The present approach suggests that the evolution of cooperation (or more specifically, benefit transmission) and other behaviors are likely to be dependent upon complex spatial and social dynamics such as these.

Research on human decision making suggests that humans can process complex information from the physical and social environment, often using heuristics that operate on this regularities in this information to produce adaptive behavior with lower computational requirements than alternatives (Gigerenzer, 2000; Gigerenzer et al., 1999). The ability of individuals to use information embedded in the environment to make adaptive decisions such as these has been called ‘ecological rationality’ (Gigerenzer et al., 1999), a term that can apply widely to the decision making rules that operate on and effects on spatial and temporal assortment.

CONCLUSION

The ultimate value of the framework presented here is that it provides a concise framework for understanding the evolution of cooperation that distinguishes among evolutionary effects, individual benefits and contingent behavior (in contrast to Bergmuller et al., 2007a; Lehmann and Keller, 2006; Nowak, 2006; Sachs et al., 2004), and synthesizes diverse approaches to the evolution of cooperation and movement. The present system classifies a large number of models of the evolution of cooperation as manifestations of a few general principles: assortment of genes in space or time and through passive or active processes.

The essence of active assortment is the ability to move or change benefit transmission based on the processing of information from the environment. Complex feedback loops can emerge from active assortment because agents can act on environmental information (such as the availability of benefits or likely proximity of kin) in ways that change the information in the environment. Individuals can respond to insufficient benefits (temporal assortment information) by moving in space (changing spatial assortment information) or respond to the proximity of likely kin (spatial assortment information) by emitting benefits (changing temporal assortment information).

This framework is not only valuable for categorizing the mechanisms that underlie the evolution of cooperation, it also suggests connections among diverse biological and social phenomena that make use of the temporal and spatial association of genes. For example, local reproduction, offspring dispersal, colonization of new areas, foraging adaptations, the contingent transmission of benefits, and changes in social organization through movement can all be conceptualized within this framework.

The ultimate value of this new conceptual system is the clarity it affords about the various processes the underlie selection and promotion of cooperative behavior. The 2x2 framework involves only two distinctions, between passive/active assortment spatial/temporal assortment, making it much more concise than previous frameworks. Perhaps most interestingly, this framework proposes that complex interactions between information processing abilities and spatial dynamics can promote the evolution of cooperation. This approach strongly suggests that the integration of population level phenomena and individual decision making rules is a fertile area of inquiry for future work on the evolution of cooperation.

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