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The Red King Effect

Evolutionary Rates and the Division of Surpluses in Mutualisms

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ABSTRACT

Mutualisms generate surpluses. Although much of the theoretical literature to date has focused on mechanisms by which cooperation is stabilized so that these surpluses can continue to be produced and enjoyed, we address a second question: how will these surpluses be distributed among the participants? We approach this question from an evolutionary game theory perspective, exploring how the coevolutionary process "selects" an equilibrium division of the surplus from among the many possibilities.

We place particular emphasis on the importance of the relative rates of evolution of the two species. Contrary to the Red Queen hypothesis, which suggests that fast evolution is favored in coevolutionary interactions, we find that slowly evolving species are likely to gain a disproportionate fraction of the surplus generated through mutualism. This occurs because on an evolutionary timescale, slow evolution effectively ties the hands of a species, allowing it to "commit" to threats and thus "bargain" more effectively with its partner over the course of the coevolutionary process.

INTRODUCTION

Mutualist partners benefit mutually, by definition. That is to say, when individuals engage in an interspecific mutualism, they enjoy benefits above and beyond what they would have enjoyed in the absence of the interaction. (Using the terminology from economics, we call these benefits the surplus generated by the mutualism.) Despite the bilaterally advantageous nature of such interactions, the participants in a mutualism rarely have entirely coincident interests. Each would benefit from altering the arrangement so as to increase its own share of the surplus at the expense of its partner. How are mutualisms established and maintained despite these conflicts? This question can be subdivided: What prevents a mutualism from breaking down as individuals find ways to exploit their partners over evolutionary time? If mutualism does not break down, what determines the allocation of the surplus among partners?

What Prevents the Exploitation of Mutualism?

To date, the majority of the empirical and theoretical studies of mutualism evolution have focused on this question. Structurally, the theoretical issue — how cooperation is maintained despite incentives to defect — is very similar to that addressed in the extensive literature on the evolution of intraspecific cooperation. Since partners are not conspecifics, however, the kin selection explanations commonly employed to explain intraspecific generosity cannot be invoked to explain the interspecific analog. Instead, investigators have typically searched for mechanisms that deter cheating (or at least ameliorate the cost of being cheated) by more direct means. Such mechanisms include reciprocal altruism, partner choice, sanctioning, and by-product mutualism or pseudoreciprocity. Bergstrom et al. (this volume) provide an overview of these alternatives. Thus, we will not consider this question in detail here.

How Will the Benefits of Mutualism Be Divided?

Far less attention has been given to the matter of what happens once the mutualistic association is somehow stabilized. (Welcome exceptions include Bowles and Hammerstein [this volume] and some of the "biological markets" literature, including Bshary and Noë [this volume].) In particular, how will the benefits from the interaction be allocated among the participants? Though a mutualistic interaction offers benefits to both species, the two species will obviously have different interests with respect to the actual division of the surplus: each would benefit from gaining a larger share.

In some cases, the goods being "traded" are provided in very different currencies and the "exchange rates" between them are essentially set by mechanistic constraints. In such cases, division of the surplus is straightforward. Cleaning mutualisms, such as those described by Bshary and Noë (this volume), provide one of the best examples. In these interactions, the cleaner gets the benefit of a ready food source, and the "client" gets the benefit of having its parasite load reduced. The potential for cheating — cleaners feeding on live tissue or clients preying on cheaters, for example — adds a degree of extra complexity, as does competition among clients for cleaners. Nonetheless, if market forces or other mechanisms do ensure cooperation between a cleaner and a client, the division of the benefits is relatively straightforward (Bshary and Noë, this volume).

The allocation of benefits, however, is not always so clear, as we can see by observing the mutualistic association between ants and lycaenid butterfly caterpillars (Pierce 1987, 2001). These caterpillars, largely protected by the ants from parasitoids (a huge contributor to mortality), enjoy enormous increases in survivorship to and during pupation (Pierce and Mead 1981; Pierce and Easteal 1986). Consequently, they can afford an extended developmental period, during which they are able to generate a sugar- and protein-rich exocrine secretion with which to purchase continued protection at the expense of a reduced rate of growth (Hill and Pierce 1989; Baylis and Pierce 1992; Pierce et al. 1987). In this situation, there is no single obvious division of the surplus. In general, then, at what rate should the lycaenids provision their ant attendants? In addition, how much should the ants "demand" in return for tending to the caterpillars?

Evolutionary Rate and the Coevolutionary Process

Here, we describe the way in which dynamic evolutionary game theory can be used to explore how surpluses will be divided among mutualist partners. We will pay particular attention to the role of evolutionary rate in determining the properties (in particular, the allocation of benefits) of mutualisms. Partners in coevolutionary interactions may evolve at different rates for a number of reasons, including differences in generation time, differences in the importance of the interaction, differences in population size, and differences in the amount of segregating genetic variation (Dawkins and Krebs 1979).

Theoretical and empirical studies of coevolution have explored the consequences of evolutionary rates and coevolutionary races in substantial detail; however, the present approach represents something of a departure from these earlier studies in its emphasis on mutualistic interactions. Most previous analyses have dealt with antagonistic coevolution, such as that between predators and prey or hosts and parasites. In these situations, species pairs become locked into "rat races" (Rosenzweig 1973) or "arms races" (Dawkins and Krebs 1979) with each rushing to evolve the upper hand in the interaction. The end result is a Red Queen process (Van Valen 1973), in which the two species each have to evolve rapidly just to keep up with one another. As Lewis Carroll wrote, "it takes all the running you can do, to keep in the same place."

Do mutualisms evolve by similar dynamical processes, with species racing to keep ahead of their partners (Herre et al. 1999)? Is a rapidly evolving species likely to fare better than a slowly evolving one? Here we describe how these questions can be addressed using an alternative approach to modeling the evolution of mutualism (Bergstrom and Lachmann 2003) and summarize new results which suggest that, in contrast to the Red Queen theory, slower rates of evolution may lead to favorable outcomes in the evolution of mutualism.

METHODS FOR MODELING MUTUALISM

Game theory is the study of decision making in a social context. As such, game theory provides a set of tools for analyzing the decision problem that an individual faces when her fate depends both on her own choices and on the choices of others. Traditionally, game theory has focused on identifying Nash (or related) equilibria: combinations of strategies for each participant such that no participant can gain from a unilateral change in strategy. Although this approach has proven to be extremely valuable in biology, many strategic situations or "games" turn out to have multiple equilibria, and the basic theory does little to distinguish among them (Samuelson 1997).

Resolving this *equilibrium selection* problem requires some sort of extension to the basic Nash equilibrium framework. One of the most successful extensions derives from the work of Maynard Smith and Price (1973). These authors studied how evolutionary processes (e.g., evolution by natural selection) would lead to the selection of certain strategies in populations of game-playing individuals. In general, this evolutionary game theory approach assumes that a population of agents play a given game against one another repeatedly.[1] The agents change their strategies at some rate, based on their own past experiences or those of others. Strategy change is assumed to be myopic, toward immediate improvement with no consideration of the long-term consequences. Agents may occasionally mutate or experiment, trying new strategies at random. Examples of such processes include evolution by natural selection in asexual or sexual populations, cultural transmission systems in which individuals copy successful neighbors, and learning processes in which individuals alter their strategies in accord with their previous payoffs.

Among these processes, the replicator dynamics plays a central role, in that (a) it corresponds to simple deterministic biological model of asexual reproduction with fitnesses proportional to expected payoffs, (b) it is relatively simple to analyze, and (c) many other processes can be shown to share with it the same equilibrium points and stability properties (Samuelson and Zhang 1992; Cressman 1997), and in some cases, even the same dynamics (Binmore et al. 1995; Schlag 1998). Throughout this chapter, we use the replicator dynamics as model of evolution by natural selection. However, the aforementioned convergence properties imply that our findings will also pertain to systems in which strategies change by other processes (e.g., learning) as well.

In many simple coevolutionary interactions, players come from two separate populations to engage in pairwise interactions. Such circumstances can be modeled using bimatrix games (Weibull 1995; Hofbauer 1996; Hofbauer and Sigmund 1998), also known as role asymmetric games (Maynard Smith 1982), in which the two populations have distinct payoff matrices and strategy frequencies. Here, we restrict ourselves to consideration of two-player bimatrix games. The simplest of these are 2 × 2 games, which can be represented by the following payoff matrix:

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[1] Though the game is assumed to be played repeatedly, most evolutionary game theory models do not endow players with the sort of individual recognition and memory of past events that are necessary to play "responsive" strategies, e.g., Tit-for-Tat. Instead, models typically focus on how strategies for playing the 1-shot game evolve over time.

	L	R
U	a, e	b, f
D	c, g	d, h

With a bit of arithmetic manipulation, we can derive the replicator dynamics for these simple bimatrix games, where the players come from two separate populations with evolutionary rates n and m respectively (Bergstrom and Lachmann 2003). Here, x is the frequency of L players in population 1, y is the frequency of U players in population 2, and $\pi(D, z)$ is the payoff to choosing strategy D when a fraction z of the other population plays strategy L:

$$\begin{aligned} \dot{x} &= mx\left(\pi(L,y) - [\pi(L,y)x + \pi(R,y)(1-x)]\right) \\ \dot{y} &= ny\left(\pi(U,x) - [\pi(U,x)y + \pi(D,x)(1-y)]\right) \end{aligned} \tag{12.1}$$

Qualitatively, these 2 × 2 games allow only a limited range of dynamic behaviors. We can see this by examining a strategically equivalent game; equivalent replicator dynamics can always be constructed by renormalizing matrix (1) so that the off-diagonal elements are zero (Hofbauer and Sigmund 1998):

	L	R
U	α, β	$0, 0$
D	$0, 0$	γ, δ

Setting $\alpha = a - c$, $\beta = e - f$, $\gamma = d - b$, and $\delta = h - g$, the evolutionary dynamics are preserved.[2] Qualitatively, (generic) 2 × 2 games afford four different types of evolutionary dynamics, characterized by what happens along each edge (Hofbauer and Sigmund 1998; see Figure 12.1).

Types I and II have only one stable equilibrium to which the dynamics always converge, and thus these games are of little interest so far as equilibrium selection is concerned. Type III has two stable equilibria, one at the upper right corner and one at the lower left corner. Type IV has no stable external equilibria, but only the mixed strategy equilibrium in the interior of the strategy frequency

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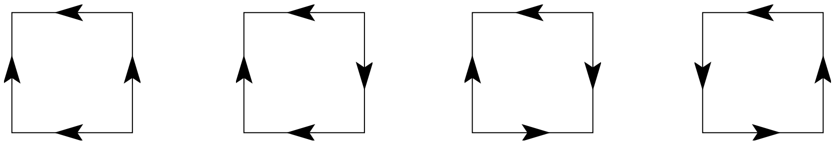
[2] Although this renormalization does not alter the evolutionary dynamics for a population playing this game, it is important to note that by renormalizing in this way we do not necessarily preserve the relative value of (U,L) and (D,R) outcomes to each player. Player 1 may receive a higher payoff from the (U,L) combination when the game is written in form (1), and a higher payoff from the (D,R) combination when the game is written in form (3). This renormalization can actually transform a coordination team game (in which both players prefer the same equilibrium) into a Battle-of-the-Sexes game (in which each player prefers a different Nash equilibrium). Here we are interested in more than just evolutionary dynamics: we wish to compare payoffs across equilibria (cf. section on Local Dynamics of Mutualism) and in structured population models for which equilibrium payoffs determine carrying capacities (see section on Higher-level Population Structure). Since the renormalized form (3) of the game does not preserve these comparisons, we will break from common convention and work with games in their unnormalized forms.



Type I	**Type II**	**Type III**	**Type IV**
$\alpha > 0 > \gamma$	$\alpha, \gamma > 0$	$\alpha, \gamma > 0$	$0 > \alpha, \gamma$
$\beta > 0 > \delta$	$\delta > 0 > \beta$	$\beta, \delta > 0$	$\beta, \delta > 0$

Figure 12.1 The four basic types of evolutionary dynamics for 2 × 2 games. Adapted from Hofbauer and Sigmund (1998).

space. Because we are interested in how the evolutionary process chooses among a set of possible equilibrium divisions of the mutualistic surplus, the games we examine here are Type III games with two equilibria.

As in previous studies, we consider interactions in which both players stand to gain from the interaction if they can find a way to cooperate. However, the approach described here differs in two respects. Rather than looking at what prevents breakdown, we examine how the gains from the interaction will be distributed between the two players, *in the absence of incentive to defect on an established cooperative arrangement*. Thus, instead of examining a Type I Prisoner's Dilemma interaction with one Nash equilibrium, we examine a Type III coordination-type game with two Nash equilibria. This provides us with a simple model that shares a common feature of many game-theoretic interactions: multiple Nash equilibria exist, but different players have different "preferences" over the set of equilibria. We would like to understand which equilibrium will be selected in an evolutionary system. Second, we go "back to basics," in the sense that we will examine only the simple one-shot 2 × 2 game dynamics. The basic rationale for doing so is simple. Regardless of the complex strategies of reward and punishment, regardless of partner choice and market function, regardless of the series of moves and countermoves involved, successful mutualistic interaction will ultimately generate a surplus, and this surplus will ultimately have to be divided. We defer the issue of how the mutualism is enforced and how bargaining proceeds, so as to concentrate on the role of the evolutionary dynamics in shaping the division of the surplus. By doing so and by choosing a simple 2 × 2 game with its small strategy space as in our model, we can examine the question of surplus division in the simplest possible context. Once we understand the workings of this system, we can extend the model in any number of ways. In the final section, we speculate on the likely outcomes of such extensions.

LOCAL DYNAMICS OF MUTUALISM

We are interested in how organisms split the surplus from a nascent mutualism. This problem is closely related to bargaining problems treated in economics (Nash 1950, 1953; Rubinstein 1982): two or more individuals seek to establish a mutually beneficial agreement (e.g., how to divide a surplus) by common consensus, but their interests conflict regarding the precise terms of the agreement (Osborne and Rubinstein 1990). Frequently in these games, many possible divisions of the surplus are stable in the Nash equilibrium sense. Given this multitude of equilibria, what sort of division should we expect to observe in practice? One can imagine a host of models to explain how such a division could take place, and indeed the study of such models is a major component of bargaining theory (Osborne and Rubinstein 1990). Although an axiomatic approach (Nash 1950) or rationality considerations (Rubinstein 1982) can resolve the many possible equilibria, it might be more appropriate to employ population-based evolutionary models to the study of mutualisms.

Then how, precisely, should we model this situation? For example, how can we model a scenario in which two individuals have to split a surplus of three units? Unfortunately, dynamic evolutionary models can be difficult to apply to full-blown bargaining scenarios because of the infinite strategy spaces of these games. Fortunately, one can learn a great deal by looking at the evolutionary dynamics of populations playing simpler one-stage games.

One of the classic one-stage games used is known as the Nash bargaining game (Nash 1953; Osborne and Rubinstein 1990). Two players have to divide a surplus of 3 units. Each player simultaneously "demands" an amount of the surplus. If the two demands sum to 3 units or less, each player gets the amount that she demanded. If the total of the two demands exceeds 3 units, each player gets 0. Because any demand from 0 to 3 is a legitimate strategy in the Nash bargaining game, even this game has an infinite space. To study the evolutionary dynamics, we will make yet another simplification and look at a "discrete" or "mini-game" form (Skyrms 1996; Sigmund et al. 2001):

	Generous	Selfish
Selfish	2, 1	0, 0
Generous	1, 1	1, 2

In this mini-game form of the Nash bargaining game, each player can demand either 1 or 2 units of the surplus; the players receive their demands so long as the two demands are compatible with a total surplus of 3 units. Let us now extend this model slightly by replacing the (1,1) payoffs to mutual generous offers with a payoff (k, k):

	Generous	Selfish
Selfish	2, 1	0, 0
Generous	k, k	1, 2

When $k = 1$, we have the Nash bargaining mini-game, as shown above. When $k = 1.5$, the entire surplus is retained and split evenly; the game becomes a Hawk–Dove game with resource benefit 1 and cost 3 of fighting. When $k = 0$, two generous offers lead to a coordination failure as severe as that resulting from two selfish ones: players suffer a complete loss of mutualistic surplus and a standard battle-of-the-sexes game results. Thus, parameter k plays an important role in determining the effect of evolutionary rate on equilibrium selection.

We begin by looking at the dynamics of this game with $k = 1$. Figure 12.2 shows a set of evolutionary trajectories for the space of strategy frequencies for species 1 on the y axis and species 2 on the x axis, under the replicator dynamics (2) with the two populations evolving at equal rates. Almost every trajectory ends at one of two resting points: the upper left corner in which species 1 enjoys a favorable division of the surplus, or the lower right corner in which species 2 enjoys a favorable division. The eventual end point is determined by the initial frequencies; the set of all points from which the dynamics lead to a given equilibrium is called the domain of attraction of that equilibrium. The diagonal line running from lower left to upper right corners represents the separatrix between the two domains of attraction. All points on the same side of this separatrix go to the same equilibrium. The horizontal line running through the middle of the strategy space separates the points at which species 2 evolves to be more generous (above this line) from those at which it evolves to be more selfish (below this line). The vertical line strikes a similar division for species 1. These two lines together partition the strategy space into four quadrants, discussed further below.

Clearly, the ultimate division of the mutualistic surplus will depend on the starting strategy frequencies in each species. Thus we cannot answer the question, “How will the surplus be split?” without knowing where the system started. Nonetheless, one reasonable measure of the likelihood of various outcomes is simply the relative size of the various domains of attraction. All else being equal, we might expect that equilibria with large domains of attraction will be reached more often than equilibria with small domains of attraction.

What determines, however, the sizes of the domains of attraction? Bergstrom and Lachmann (2002) show that both the game payoffs and the relatively evolutionary rates matter. In particular, the relatively evolutionary rates of the two species determine the way that the separatrix curves across the strategy space.

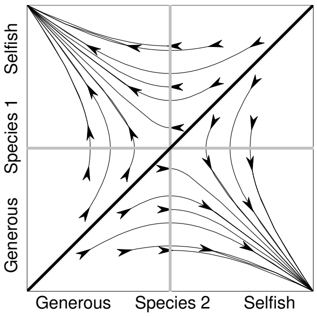


Figure 12.2 Evolutionary trajectories when $k = 1$. Horizontal and vertical lines show the places at which the change in strategy frequency switches direction for players 1 and 2, respectively. Diagonal is the separatrix between the two domains of attraction.

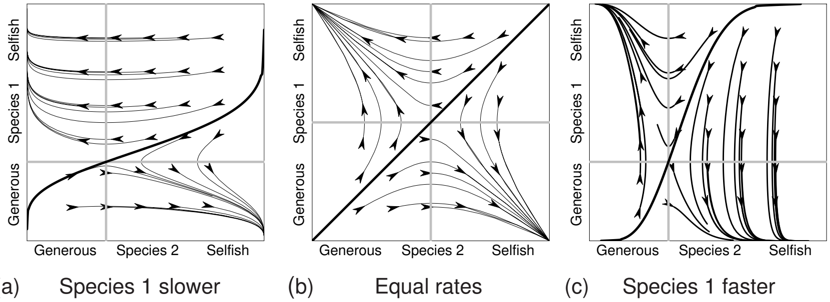


Figure 12.3 The effect of evolutionary rate on domains of attraction when $k = 1.5$: (a) species 1 evolves eightfold slower than species 2; (b) equal rates of evolution; (c) species 2 evolves eightfold slower. The slower that species 1 evolves, the larger the domain of attraction around its favored equilibrium at the upper left-hand corner.

Depending on the payoffs of the game, this can either increase or decrease the domain of attraction for the slower player. Figure 12.3 shows the strategy space and evolutionary dynamics for $k = 1.5$. Here the domain of attraction of player 1's favored equilibrium (the upper left corner) increases as player 1's relative rate of evolution decreases. This is the first manifestation of what we call the "Red King effect."

Note that as species 1 evolves at an increasingly slower rate, intense movement across the strategy space occurs along the horizontal axis. This strategy change occurs as the result of evolutionary change by species 2. This increases the fraction of the upper right-hand quadrant that goes to species 1's favored equilibrium, while decreasing the fraction of the lower left-hand quadrant. Relative evolutionary rates do not matter in the upper left- and lower right-hand quadrants; any point in either of these quadrants goes to the equilibrium in the same quadrant regardless of evolutionary rates.

Thus, the effect of evolutionary rate on the size of domains of attraction depends on the chance that the starting point is in the lower left quadrant versus the upper right quadrant. As summarized by Figure 12.4, the fast-evolving species "gets" the lower left quadrant and "loses" the upper right one.[3]

What determines, however, the quadrant in which the coevolutionary process is likely to begin? One important factor will be the size of each quadrant. As k increases, the area of the upper right quadrant — where slow evolution is favored — also increases. Indeed, the slowly evolving species will have a larger domain of attraction around its favored equilibrium whenever $k > 1$, whereas the

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[3] Our results may explain a curious observation reported by Doebeli and Knowlton (1998; see also Figure 3C therein). In their simulations of mutualism evolution, based on an iterated Prisoner's Dilemma model, they found that the more slowly evolving species received higher payoffs.

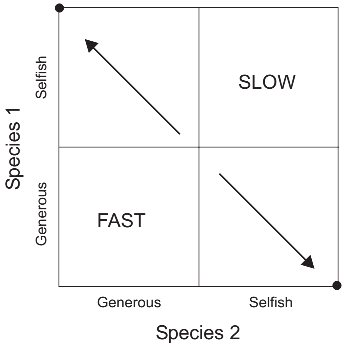

Figure 12.4 Summary of local dynamics. In the upper left and lower right quadrants, all evolutionary trajectories reach the upper left and lower right equilibria (black dots) respectively. In the upper right quadrant, the slow species reaches its favored equilibrium; in the lower left quadrant, the fast species reaches its favored equilibrium.

faster-evolving species will have a larger domain of attraction when $k < 1$ (Bergstrom and Lachmann 2003).

This result makes intuitive sense in light of bargaining theory. In bargaining games, it is well known that there may be a strategic advantage to "having one's hands tied" during bargaining. This is valuable because threats of a constrained player become more credible, while threats against this player are rendered ineffective. Since susceptibility to threats often acts as a major determinant of the strength of one's bargaining position, this is a significant advantage.

The Red King effect can be seen as simply this: a slowly evolving species has its hands tied in the coevolutionary interaction by which division of the surplus is "negotiated." Here the bargaining process does not take place within a single play of the game, but rather occurs over the course of the coevolutionary interaction between the players. In other words, the coevolutionary process can be viewed as a bargaining process through which the two species arrive at an equilibrium to the Nash bargaining game through a series of evolutionary moves and counter moves. In this bargaining process, fast evolution does not allow a species to outrun a partner — it simply causes this species to yield to whatever threats are made. This is captured by the local dynamics described earlier.

Of course, the initial proposals brought to the table by the negotiating parties will also have a major impact on the outcome of a negotiation. In the mutualism example considered here, if both species initially ask for more than their share of the proverbial pie, susceptibility to threat will be important. What will be the initial proposals that the species bring to the table? We explore this question below.

HIGHER-LEVEL POPULATION STRUCTURE

Evolutionary game theory typically assumes that the populations of players materialize fully formed and out of thin air at the beginning of the evolutionary process under consideration. Obviously, the real situation is somewhat more complicated. When populations are formed anew, their members must have come from *somewhere*, and this somewhere may have had a significant influence on the strategies that they bring with them to the new population.

Thus, when potential mutualists come together in a given location, what should we imagine about their past histories, their distribution of strategy choices, and so forth? One straightforward approach is to assume that upon founding a new patch, individuals use the same initial strategies that they had employed in their natal patches. We can model this by looking at a structured population of players, in which the dynamic process of strategy change treated above occurs in parallel in a set of distinct local patches. Each local patch then sends out migrants to join existing patches or to found new patches. There is an extensive literature on the workings of such structured-population models (Bergstrom 2002). Here we have selected to work with one of the simplest of these models, the haystack-type model (Maynard Smith 1964; Cohen and Eshel 1976). We expect that other structured population models will yield qualitatively similar results in most cases.

Our haystack model works as follows. The environment is divided into a set of local patches. Every "season," a small number of founder individuals of each the two species colonize each patch. Once colonization has occurred, within each patch during the course of a single season the strategy frequencies change according to the local dynamics characterized in the previous section.

Note that these local dynamics characterize changes in strategy frequencies but not in population size. In the structured population model, we are also interested in how population sizes change according to the strategies played. For simplicity, we will assume that within the course of a single season, each species grows to a carrying capacity in each patch. The exact magnitude of the carrying capacity for each species reflects the "favored" or "disfavored" nature of the equilibrium reached in the patch. That is, a species will have a higher carrying capacity in a given patch if it reaches its favored equilibrium than if it reaches its disfavored equilibrium. We will assume that each season is sufficiently long that every local subpopulation reaches an equilibrium with respect to strategy frequencies, so that we only need to specify carrying capacities for the two equilibria and not for any out-of-equilibrium combinations of strategy frequencies.

At the end of the season, patch boundaries are erased. Individuals disperse, and subpopulations are formed of individuals chosen at random from the global population. A new season then begins and the process starts anew.

Figure 12.5 shows how the domain of attraction around each equilibrium shifts as we take into account the higher-level population structure. Under local dynamics, domains of attraction are equal in size for $k = 1$. However, global dynamics favor slowly evolving species. This species (species 2) has a larger domain of attraction around its favored equilibrium at the lower right-hand corner.

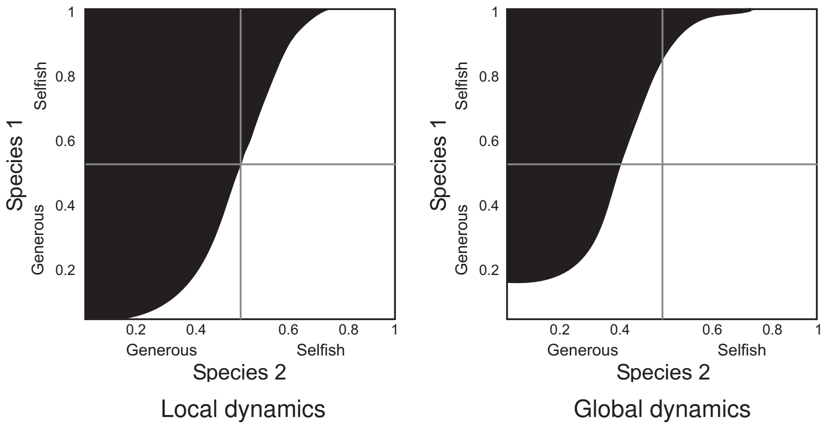

Figure 12.5 Domains of attraction in the local dynamics and for the higher-level population structure with $k = 1$, when species 1 evolves 8-fold faster than species 2. For the global dynamics, each new patch is founded by 9 individuals and each species' carrying capacity at its favored equilibrium is 4 times that at the disfavored equilibrium.

Why does this happen? Consider the process by which a new subpopulation is formed. Members arrive from other subpopulations. Subpopulations at the equilibrium where species 1 is favored, i.e., where species 1 is playing selfishly, have a higher carrying capacity for species 1 and thus contribute more species 1 individuals than do subpopulations where species 2 is favored. Therefore, the odds are that a majority of incoming species 1 individuals will have arrived from a subpopulation in which they were playing selfishly. Similarly, a majority of incoming species 2 individuals will most likely have come from a subpopulation in which *they* were playing selfishly. Consequently, when a new subpopulation is first established, the majority of players therein are likely to be playing selfishly: the newly formed population is likely to begin with a set of strategy frequencies belonging to the shaded quadrant in Figure 12.6. We know that local dynamics favor the slow evolver under these circumstances. Thus in each newly formed subpopulation, slowly evolving species will have a relative advantage.

We can visualize this argument as follows: if a proportion s of the patches reaches an equilibrium that favors species 1, and $(1 - s)$ reach one that favors species 2, and the relative size of the carrying capacities for species 1 and 2 are α and β, then at the end of a season the proportion of individuals of species 1 playing the selfish strategy in the global pool will be $s/(s + (1 - s)\alpha)$, and the proportion of species 2 playing the selfish strategy will be $(1 - s)/(1 - s + s\beta)$.

Thus the relative frequencies of the strategy types in the global pool will lie somewhere along the dark curve depicted in Figure 12.6. This curve passes through the upper-right quadrant, where slow evolution is favored, and not through the lower-left one, where fast evolvers are favored.

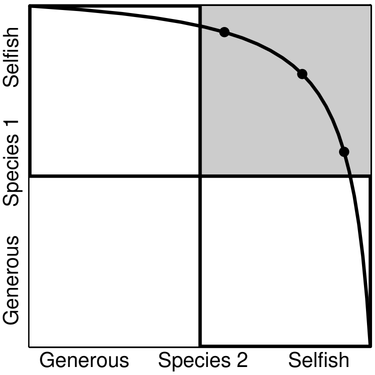

Figure 12.6 Summary of global dynamics. Each subpopulation ends with either species 1 playing generous and species 2 playing selfish, or visa versa. The fraction of subpopulations in each state determines the expected frequencies in each new subpopulation at the start of the next season. Recall that local dynamics favor slowly evolving species in the shaded upper right quadrant. Carrying capacity ratios are $\alpha = 4$ and $\beta = 4$.

Once again we can see these results in light of bargaining theory. As mentioned above, the initial proposals brought to the table by the negotiating parties will also have a major impact on the outcome of a negotiation. In the mutualism example considered here, if both species initially ask for more than their share of the proverbial pie, susceptibility to threat will be important. But what will be the initial proposals that the species bring to the table? We have argued that in coevolutionary interactions, population structure bears critically upon this question. If new patches are formed by immigrants from other patches, individuals will come together prepared by evolution to pursue a division similar to that which they were receiving in their previous patches. When carrying capacity of a patch is affected by the division of mutualistic surplus, most players entering a new patch will arrive "demanding" more than half of the surplus. This situation (when parties do not initially agree on the division because both expect a majority share) is precisely when it pays to have one's hands tied in the negotiations.

DISCUSSION

Beyond Mini-games

Thus far, we have discussed the evolutionary dynamics associated with populations playing simple 2 × 2 games. What happens when the interactions in question are broader in scope? What happens, for example, when individuals of the two species are playing the full Nash bargaining game in which each can demand any amount from 0 to 3?

For this game, a full analysis of the local dynamics, which take place on an infinite-dimensional simplex and which will depend on many particulars of the model, would be very difficult. Nonetheless, analogy to the 2 × 2 game provides us with a good sense of how evolution will proceed. In the full game, just as in the 2 × 2 counterpart, slow evolution will be favored when players are demanding too much, so that the sum of the demands exceeds 3 and bargaining breaks down. By starting with a large demand and evolving slowly, one species forces the other to "yield" and to demand less than half of the total. Fast evolution will be favored when the players begin by demanding less than 3, because the fast evolver will be able to adjust its demand to claim the remainder of the 3 units.

Moreover, as in the 2 × 2 version of the game, the higher-level population dynamics will ensure that players come together with demands in the region where slow evolution is favored: these dynamics will act to bring together players who are demanding too much, rather than too little. Imagine a global population composed of subpopulations which have reached a range of different equilibrium arrangements: $(\delta, 3-\delta), (2\,\delta, 3-2\,\delta), \ldots, (3-\delta, \delta)$. At the beginning of a new season, the majority of species 1 players will come from populations where species 1 had a high carrying capacity, i.e., populations where species 1 was receiving a relatively large fraction of the total benefits. Similarly, species 2 players will come from populations in which species 2 had a high carrying capacity, i.e., populations where species 2 was receiving a relatively large fraction of the total benefits. Thus the large majority of the newly founded subpopulations will be composed of players who together demand a total exceeding 3. This is the region in which slow evolution is favored; consequently we expect the higher-level population structure to favor slow evolution in the full Nash bargaining game as well.

Interactions among Humans

Here we have focused primarily on mutualistic associations among nonhuman agents evolving by natural selection. Will similar processes apply to human interactions? We argue, they may. Various processes of strategy change, including learning and copying behaviors, can yield qualitatively similar outcomes to those observed in systems that change according to replicator dynamics.

This is all good and well, but human beings (or even real-world mice) do not live in haystacks with the sort of structure modeled above. Can analogous higher-level selection processes nonetheless operate? We stress that these sorts of structured-population dynamics require neither small founding populations (see Bergstrom and Lachmann 2003) nor that some sort of life-or-death group selection take place. Such a process only requires that *the majority of players in each new round come from places where they did well in the previous round.* This could occur for many reasons. For example, in human interactions, players may decide whether to continue participating in some two-sided interaction based on their past experience. Players who have done well may continue to engage in the interaction, whereas those who have done poorly may choose to opt out and do something else instead. Under certain circumstances, players who reached the favored outcome will return to play again, players who reached the disfavored outcome will take the outside option, and the conditions will be met for the Red King effect to operate on the higher level of population structure.

This phenomenon may be rather general to human interactions, such that the individuals who choose to participate at any given time are either new to the interaction in question or have a past record of success. Thus individuals choosing to play may have a higher-than-average expected return from the game. In bargaining games of this sort, this means that the individuals choosing to participate will enter each new situation asking for more than an even share.

SUMMARY

The study of interspecific mutuality allows biologists an unparalleled opportunity to explore the mechanisms beyond kin selection by which coordination and cooperation can evolve. Although much of the theoretical literature to date has focused on mechanisms by which cooperation is stabilized, we addressed the issue of how benefits that arise as a consequence of mutualism are distributed among the participants. We have given particular attention to the role of evolutionary rate in determining coevolutionary outcomes. Most notably, recent results suggest that, contrary to the Red Queen hypothesis, slow evolution may actually lead to favorable outcomes in some coevolutionary interactions.

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