

Symbiosis emergence and abandonment in nature: a coordination game approach¹

Simon A. Levin²

Ted Loch-Temzelides³

2025

Abstract

We employ an n -player coordination game to model mutualism emergence and abandonment. We illustrate our findings in the context of the host–host interactions among plants in plant-mycorrhizal fungi (MF) mutualisms. The coordination game payoff structure captures the insight that mutualistic strategies lead to robust advantages only after such “biological markets” reach a certain scale. The game gives rise to three types of Nash equilibria, which correspond to the states derived in studies of the ancestral reconstruction of the mycorrhizal symbiosis in seed plants. We show that all types of Nash equilibria correspond to steady states of a dynamical system describing the underlying evolutionary process. We then employ methods from large deviation theory on discrete-time Markov processes to study stochastic evolutionary dynamics. We provide a sharp analytical characterization of the stochastic steady states and of the transition dynamics across Nash equilibria and employ simulations to illustrate these results in special cases. We find that the mutualism is abandoned and re-established several times through evolutionary time, but the mutualism may persist the majority of time. Changes that reduce the benefit-to-cost ratio associated with the symbiosis increase the likelihood of its abandonment. While the mutualism establishment and abandonment could result from direct transitions across the mutualistic and non-mutualistic states, it is far more likely for such transitions to occur indirectly through intermediate partially mutualistic states. The MF-plant mutualism might be (partially or fully) abandoned by plants even if it provides overall superior fitness.

¹Correspondence to [tedt@rice.edu]

²Princeton University

³Rice University

1 Introduction

Though mutualisms are common in nature, there is no general theory on whether they will be stable once they have evolved and on what drives the observed repeated transitions between mutualistic and non-mutualistic states. For example, pollination mutualisms in angiosperms appear to be lost frequently (Culley et al. 2002; Friedman 2011), whereas the mutualistic symbiosis between plants and nitrogen-fixing bacteria appears to persist over evolutionary time (Werner et al. 2014). Other examples of mutualisms that are formed, dissolved, and possibly re-established over time include the following.

Ant–Plant Mutualisms

The symbiosis between ants and plants involves many species throughout the tropics and was one of the first mutualisms to be investigated by ecologists. Plant–insect mutualisms have arisen and been lost repeatedly (Bronstein et al, 2006). Many *Acacia* species have mutualistic relationships with ants (e.g., *Pseudomyrmex*), providing shelter and food to several species of ants who in turn defend the trees from herbivores. Palmer et al. (2008) investigated the effects of large mammalian herbivores on an ant-*Acacia* mutualism in an African savanna. In the absence of browsing by large herbivores, *A. drepanolobium* trees stopped producing nectar and hollow thorns, essentially abandoning the mutualism when ant protection became less beneficial. Such mutualisms can re-evolve if herbivore threats return or as host trees develop and abandon repeated symbiotic relationships with different competing species of ants (Palmer et al. 2013).

Coral–Algae (Zooxanthellae) Mutualisms

Scleractinian (stony) corals form symbioses with a wide range of symbiotic algae, including phototrophic dinoflagellates in the genus *Symbiodinium*, for nutrients via photosynthesis. Under thermal stress, bleaching might offer an opportunity for reef corals to rid themselves of suboptimal alga, temporarily abandoning the symbiosis. As the coral host depends on photosynthate for nutrition, a prolonged breakdown of the symbiosis can lead to coral death (Baker, 2003). However, corals may re-establish the mutualism, sometimes with more heat-tolerant algae variants (Baker, 2001). Thus, switching to more thermally tolerant symbionts has the potential to benefit coral reefs that face increasingly frequent mass bleaching due to climate change. Boulotte et al (2016) found evidence for symbiont switching in reef-building corals, with two de novo acquired thermally resistant *Symbiodinium* types, suggesting

that this switching may have been driven by consecutive thermal bleaching events. While these changes involve relatively short horizons, they do correspond to transitions across different equilibrium outcomes and can be modeled using coordination games.

Land plant-arbuscular mycorrhizal fungi mutualisms

Land plant-arbuscular mycorrhizal fungi mutualisms are sometimes abandoned, partial, re-established, etc. over evolutionary time (Werner et al. 2018). Figure 1 represents derived evolutionary transitions rates across plant-mycorrhizal fungi mutualistic states (**AM**), non-mutualistic states (**NM**), and partially mutualistic states (**AMNM**) for monocots (Maherali et al. 2016). The number in parentheses indicates the percent of species in that state, while the number next to each arrow indicates the transition rate in numbers of transitions per million years. In what follows, we will attempt to understand the transitions between mutualistic, partially mutualistic, and non-mutualistic states as the outcome of an evolutionary process operating on an underlying *coordination game*. The numbers in parenthesis will then correspond to the fraction of time spent by plants in each respective state over a long time horizon.

Our *coordination game* captures the qualitative features of the relative payoffs associated with the symbiosis and its abandonment. We will then employ methods from large deviation theory to characterize analytically the evolutionary dynamics and the associated long-run outcomes of an evolutionary game. As an illustration, we will frame the model in the context of the plant-mycorrhizal fungi (MF) mutualisms (Maherali et al. 2016). More precisely, we model the host plants as playing a coordination game in evolutionary time. As in Halloway et al (2022), we will take the behavior of their MF as fixed and in what follows we will concentrate on the host interactions between the seed plants.

Previous studies of mutualism persistence and abandonment using evolutionary game theory have concentrated on the role of cheating; see, for example, Bronstein (2001), Ferriere et al (2002), Bronstein (2006), and Jones et al (2015). Here we provide an alternative game-theoretic explanation where mutualism abandonment can take place even in the absence of cheating, for example, in cases where effective punishment strategies have eliminated any advantage to cheaters. Coordination games offer an interesting paradigm, as they give rise to multiple Pareto ranked Nash equilibria (Nash, 1951).⁴ They

⁴Two equilibria are Pareto ranked if one yields strictly higher payoffs for all players

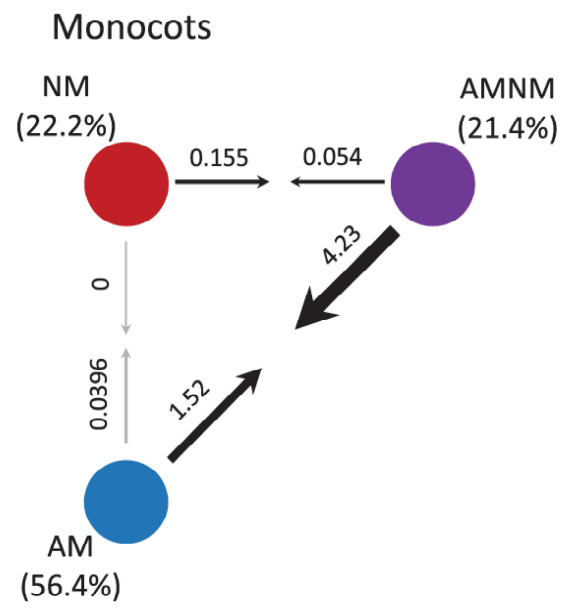


Figure 1: Transitions between mutualistic (AM), partially mutualistic (AMNM) and non-mutualistic (NM) states (Figure from Maherli et al, 2016)

have been used in economics and the social sciences to model market creation, new technology adoption, economic recessions, and social conventions, among other phenomena. In the context of biological mutualistic markets (Noë and Hammerstein, 1994, 1995) the coordination game payoff structure captures the insight that such markets cannot operate effectively, unless they reach a certain participation size or “*thickness*.” That is, establishing or reintroducing a mutualism might not be viable unless it reaches a certain scale in terms of the number of individuals participating. Once that threshold is reached, mutualistic strategies can lead to robust advantages. This can be, for example, due to diversification and the ability to adjust to changes in external conditions, both of which require the biological market to operate at a certain minimal scale.

The model gives rise to three types of Nash equilibria, which match the states derived in the formal ancestral reconstruction of the mycorrhizal symbiosis in seed plants in Maherali et al (2016). The first corresponds to the state of full plant-mycorrhizal fungi mutualism (**AM**). The second corresponds to a complete mutualism abandonment (**NM**). Finally, the third type captures mixed equilibria of partial mutualisms (**AMNM**). In terms of dynamics, all three types of Nash equilibria correspond to steady states of the deterministic dynamical system describing the underlying evolutionary process. Introducing random perturbations (“mutations”) allows us to study the resulting stochastic evolutionary dynamics. Employing techniques from large deviation theory in the study of discrete-time Markov processes; see, for example, Freidlin and Wentzell (1984), Kandori et al (KMR, 1993), Young (1993), Ellison (2000), Blume et al (2003), and Dembo and Zeitouni (2009), we provide a sharp analytical characterization of the stochastic steady states (ergodic distributions) and of the transition dynamics across Nash equilibria in evolutionary time. We use simulations to illustrate these results in special cases.

Our main finding is that the evolutionary coordination game qualitatively captures the main features of the time evolution of the plant-MF symbiosis discussed in Maherali et al (2016). Notably, our model is consistent with the following observations: *(i)* the mutualism is abandoned and re-established several times through evolutionary time, *(ii)* the mutualism persists the majority of time in the seed plant-mycorrhizal symbiosis, *(iii)* environmental and other changes that lower the benefit-to-cost ratio of a symbiosis increase

than the other.

the likelihood of its abandonment and can therefore serve as indicators of such transitions, and (iv) while the symbiosis establishment and abandonment could result from direct transitions across the **AM** and the **NM** states, it is far more likely for such transitions to occur indirectly through intermediate **AMNM** states. Interestingly, the MF-plant mutualism might be (partially or fully) abandoned even if it is overall superior for plant fitness. Concepts from the theory of large deviations tailored to discrete-time Markov chains, notably the *modified co-radius* (Ellison, 2000), formalize the notion that large evolutionary changes driven by random mutations are more likely when they can be achieved by passing through a number of “transient” steady states. We characterize conditions that guarantee that over a long enough time horizon, the system spends most of the time in the **AM** Nash equilibrium. However, the system will eventually escape and reach another limit set, before it escapes again over evolutionary time. The resulting dynamics also explains why the **AM** state is reached more frequently through the intermediary **AMNM** state.

Archetti et al (2011) discuss applications of economic game theory, including signalling, principal-agent models, and models involving public goods, to the study of mutualisms. They do not, however, discuss stochastic evolutionary dynamics in the context of coordination games, which is the focus of our study. McNickle and Dybzinski (2013) provide an accessible general introduction to some of the concepts of game theory for plant ecologists. Xu et al (2021, 2023) employ landscape-flux methods from non-equilibrium statistical mechanics to investigate transitions across locally stable steady states in an ecological context. Our approach differs from theirs in two main ways. First, the dynamics in our model is driven by an underlying coordination game whose Nash equilibria are in an one-to-one correspondence with the steady states of the dynamical system employed to capture the evolution of a mutualism. Second, although the model gives rise to multiple steady states, we employ large deviation Markov chain methods to derive a sharp characterization of the long-run behavior of the system in the presence of infrequent random perturbations, or “mutations.”

Of special interest for our analysis is the study by Halloway et al (2022). They employ a game-theoretic framework to study the symbiosis between plants and their microbial symbiotes. Like us, they focus on host–host interactions among host plants. Their analysis is based on 2-player games, where they investigate the possibility of coexistence of mutualist and non-mutualist strategies in the plant population. The payoff matrix in their game captures

the insight that a larger fraction of symbiotic host plants can make the microbial symbiosis *less* beneficial if resources are limited, thus reducing the usefulness and frequency of mutualism. Their model predicts that mutualist and non-mutualists frequently coexist at the same time within a population. The coordination game structure, in our n -player coordination game attempts to capture a different force, namely that once a certain participation threshold needed to establish the biological market is reached, the benefits of a mutualism *increase* in the number of participants. Like in other markets, this would be true if, for example, increased market thickness results in more reliable supply and resilience to outside shocks. Employing techniques from stochastic evolutionary dynamics allows for multiple *over time transitions* across the **AM**, **NM**, and **AMNM** Nash states in our model.

In what follows, after discussing the coordination game structure, we will introduce deterministic, followed by stochastic evolutionary dynamics. The latter will result in repeated transitions across the static Nash equilibria over evolutionary time, mimicking the historical record of the repeated abandonment and reintroduction of the biological market mutualism. We then use simulations to illustrate these results in special cases. The SI Appendix contains a formal treatment of the stochastic evolutionary dynamics.

2 The n -player coordination game and Nash equilibrium

To understand the processes through which the mycorrhizal symbiosis is maintained or lost, Maherali et al (2016) reconstructed its evolution using an approximately 3,000-species seed plant phylogeny integrated with mycorrhizal state information. For our purposes, their analysis identifies the following qualitative features: *(i)* **AM** symbiosis is persistent; *(ii)* direct transitions between **AM** and **NM** states are rare, indicating that evolutionary forces favor stasis when one of these states is reached, and that mutations that allow transitions between states occur at a relatively low rate; *(iii)* reversions from **AMNM** back to **AM** are an order of magnitude more likely than transitions to the **NM** state, suggesting that natural selection favors **AM** symbiosis over mutualism abandonment; and *(iv)* the transition rates from **NM** to **AMNM** are higher than the reverse, thus, loss of mycorrhizal symbiosis can be recovered through the mixed **AMNM** states. We will

demonstrate that the coordination game-theoretic framework we will introduce provides a mechanism that captures several of these features.

We consider the plant-MF mutualism as an example of a “*biological market*” (see Noë and Hammerstein, 1994, 1995), in which plants supply carbon to MF in exchange for nutrients. Like any other market, biological markets require a certain level of “thickness” to be viable. In other words, if participation is not sufficiently large, the market is unlikely to be a reliable source of the desirable commodities, as small changes, for example in underlying environmental conditions, could lead the mutualism to collapse in favor of alternative ways to obtain the necessary commodities. This feature is captured by the notion of a *coordination game*. In what follows, we will employ a “partial equilibrium” approach. We will take the behavior of the fungi as exogenously given, and will concentrate on the game played by a population of plants. Like the prisoner’s dilemma game, the coordination game paradigm is a well-studied model in economics, but not often studied in biology. Unlike the prisoner’s dilemma game, which obtains a unique Nash equilibrium in dominant strategies, a coordination game gives rise to multiple Nash equilibria. These equilibria have a natural correspondence to the observed outcomes of the biological market mutualism. The first Nash equilibrium corresponds to the outcome where the symbiosis is established (**AM**). The second Nash equilibrium corresponds to the outcome where the symbiosis is abandoned (**NM**). It is worth pointing out that both pure-strategy Nash equilibria are *strict*, therefore they constitute evolutionary stable strategies (ESS).⁵ In the case of the **AM** equilibrium, a mutant that abandons the well-established symbiosis would be worse off. Similarly, in the **NM** equilibrium, where the symbiosis is non-existent, a mutant (or indeed a small number of mutants) would not be able to create the market thickness necessary for the symbiotic biological market to take off. Finally, the mixed Nash equilibria (**AMNM**) correspond to cases where the symbiosis is pursued by a sufficient number of plants to create a (barely) functional biological market, which is as good as other alternatives. In this case, only a fraction of the plant population pursues the symbiosis. We remark that the **NM** Nash equilibrium is an ESS even though the **AM** equilibrium is associated with a higher plant population fitness. Thus, coordination games can explain why evolution might lead to mutualism abandonment and stable outcomes of inferior overall fitness even

⁵A Nash equilibrium is strict if each player’s strategy is their unique best response, meaning any deviation would make them strictly worse off.

in the absence of “cheating.”

Formally, we consider a symmetric normal-form game, $\Gamma = \langle N, S^i, u^i \rangle$, with n identical players and two strategies. The set $N = \{1, 2, \dots, n\}$ denotes the set of players. The n players correspond to seed plants of a given type. Let $S = \{s_1, s_2\}$ be the set of pure strategies; s_1 stands for “engage in plant-mycorrhizal fungi mutualism (**AM**),” while s_2 stands for “do not engage in plant-mycorrhizal fungi mutualism (**NM**).” The payoff functions for each player are identical, meaning $u^i = u$ for all $i \in N$. The payoff function u is defined as follows. Let $\mathbf{s} = (s^1, s^2, \dots, s^n)$ be a *strategy profile*; i.e., a vector describing the strategies played by each player i , where $s^i \in \{s_1, s_2\}$, for each i . We use $\mathbf{s}^{-i} = (s^1, \dots, s^{i-1}, s^{i+1}, \dots, s^n)$ to denote the strategy profile of everyone but player i . We have the following.

Definition 1: A strategy profile $\hat{\mathbf{s}}$ is a pure strategy Nash equilibrium for Γ if, for all i , $u^i(\hat{\mathbf{s}}) \geq u^i(s^i, \hat{\mathbf{s}}^{-i})$, for all $s^i \in S^i$. A Nash equilibrium $\hat{\mathbf{s}}$ is strict iff for all i , $u^i(\hat{\mathbf{s}}) > u^i(s^i, \hat{\mathbf{s}}^{-i})$, for all $s^i \in S^i$.

Let z be the number of players employing strategy s_1 ; thus $n - z$ is the number of players employing strategy s_2 . The payoff for each player depends on the number of players employing each strategy. Let $u(s_i, z)$ denote the payoff for a player employing strategy s_i when z other players also employ s_1 . Formally, we have the following.

Definition 2: The game Γ is a coordination game if the following conditions hold:

(C1) Highest payoffs for coordination in strategy s_1 :

$$u(s_1, n) > u(s_2, n - k), \quad \text{for all } 0 \leq k \leq n \quad (1)$$

(C2) Increasing payoffs with coordination in either strategy:

$$u(s_1, z+1) \geq u(s_1, z) \quad \text{and} \quad u(s_2, z) \geq u(s_2, z+1), \quad \text{for all } 0 \leq z < n-1 \quad (2)$$

(C3) Coordination threshold region:

$\exists z_*, z^*$ such that

$$u(s_1, z) > u(s_2, z), \quad \text{for all } 0 < z^* < z \leq n-1 \quad (3)$$

$$u(s_1, z) = u(s_2, z), \quad \text{for all } 0 < z_* \leq z \leq z^* < n-1 \quad (4)$$

$$u(s_1, z) < u(s_2, z), \quad \text{for all } 0 \leq z < z_* < n-1 \quad (5)$$

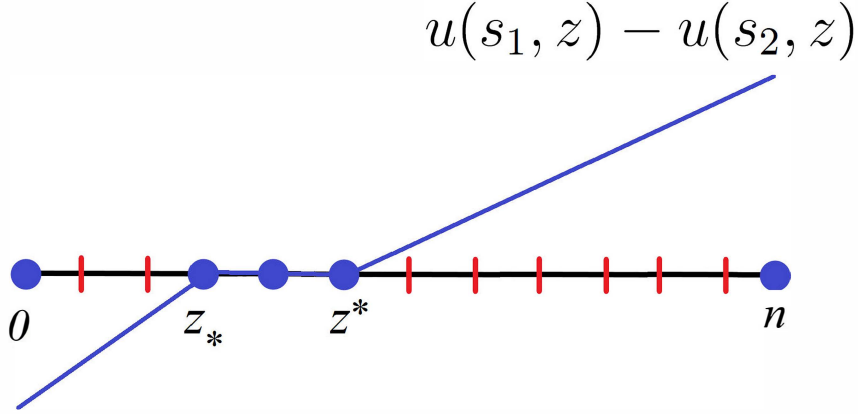


Figure 2: Coordination game: payoffs and basins of attraction

Condition (C1) implies that strategy profile $\hat{s}_1 = (s_1, \dots, s_1)$ is the Pareto optimal pure strategy Nash equilibrium of the game. Condition (C2) implies that the payoff from choosing strategy s_1 (respectively s_2) weakly increases as more players choose strategy s_1 (respectively s_2). Condition (C3) implies the existence of a set of mixed Nash equilibria indexed by $z \in [z_*, z^*]$. The two pure strategy Nash equilibria of the game $\hat{s}_1 = (s_1, \dots, s_1)$ and $\hat{s}_2 = (s_2, \dots, s_2)$ are strict (therefore, ESS). The thresholds z_* , z^* will play an important role when we discuss dynamics, as they define the basins of attraction of the respective Nash equilibria. More concretely, when $z > z^*$ enough plants coordinate on the symbiotic (**AM**) strategy to make it the one providing higher fitness. In contrast, when $z < z_*$ the symbiosis is not viable, as it is not pursued by enough plants, making symbiosis abandonment (**NM**) the more successful strategy. Finally, $z \in [z_*, z^*]$ represents the mixed set of states (**AMNM**) where the symbiosis is pursued by just enough plants for the relative payoffs of the two strategies to be effectively equal.

Figure 2 gives an illustrative example of the difference in payoffs, $u(s_1, z) - u(s_2, z)$, that is consistent with the coordination game assumptions. The payoff difference between strategy s_1 and strategy s_2 is positive for high values

of z , and negative for low values of z . This results in the two pure-strategy Nash equilibria at $z = 0$ and at $z = n$. Note that for $z \in [z_*, z^*]$ we have $u(s_1, z) - u(s_2, z) = 0$, thus, states $z \in [z_*, z^*]$ correspond to mixed Nash equilibria. We shall return on this example later, after we introduce dynamics.

3 Evolutionary dynamics

We now turn to the relationship between Nash equilibria and the steady states of a dynamical system describing the underlying evolutionary process taking place in discrete time, $t = 0, 1, 2, \dots$. The state, z_t , gives the number of players adopting strategy s_1 at time t ; $z \in Z = \{0, 1, \dots, n\}$. The state evolution is described by a dynamical system:

$$z_{t+1} = b(z_t) \tag{6}$$

The function $z_{t+1} = b(z_t)$ gives the strategy representation in the population at $t + 1$, given that the time t state is z_t . We assume the following weak monotonicity "Darwinian" property and boundary conditions (see, for example, KMR, 1993):

$$\begin{aligned} \text{sign}(b(z) - z) &= \text{sign}[u(s_1, z) - u(s_2, z)], \text{ if } 0 < z < n \\ b(0) &= 0, \quad b(n) = n \end{aligned} \tag{7}$$

In words, the Darwinian property only requires that the more successful strategy increases its representation in the population in the next period. Examples of such dynamics include the (*myopic*) *best reply dynamic*, often used in economics:

$$BR(z) = \begin{cases} n, & \text{if } u(s_1, z) > u(s_2, z) \\ z, & \text{if } u(s_1, z) = u(s_2, z) \\ 0, & \text{if } u(s_1, z) < u(s_2, z) \end{cases} \tag{8}$$

and the *replicator dynamic* used in biology:⁶

⁶The familiar continuous-time version of the replicator dynamic would read: $\dot{z} = z[u(s_1, z) - \bar{u}(z)]$, where $\bar{u}(z)$ is the average payoff over all strategies given population configuration z . In other words, a strategy that results in higher than average fitness increases its representation in the population over time, and vice versa; see, for example, Taylor and Jonker (1978), Maynard Smith (1982), Hofbauer and Sigmund (1998).

$$B(z) = z \left[\frac{u(s_1, z)}{zu(s_1, z) + (n - z)u(s_2, z)} \right] \quad (9)$$

In the context of a coordination game, any deterministic dynamical system satisfying the above monotonicity property has two pure steady states, 0 and n , as well as mixed steady states $z \in [z_*, z^*]$, corresponding exactly to the pure (**AM**, **NM**) and the mixed (**AMNM**) Nash equilibria of stage game, respectively. The long-run behavior of the deterministic dynamic depends on the initial distribution across states. Initial states z_0 such that $z_0 > z^*$ will converge to the **AM** steady state, while initial states z_0 such that $z_0 < z_*$ will converge to the **NM** steady state (see Figure 2). Furthermore, a deterministic system does not permit transitions across steady states, which are the focus of our analysis.

The dependence on initial conditions is resolved if noise or “mutations” are introduced into the system. We assume that with probability ϵ , each player mutates, playing each strategy with probability $1/2$. Mutations are assumed to be *iid* across players and time. This yields a stochastic dynamical system on the finite state space Z . The associated stochastic evolutionary dynamics gives rise to a Markov chain with a unique invariant distribution, $\mu(\epsilon)$, for any given rate $\epsilon > 0$. In theoretical analysis it is standard to pay particular attention to the support of the limit distribution $\mu(\epsilon)$ when ϵ approaches zero. We will refer to sets in the support of the limit distribution as *stochastically stable states*.

A set of states $Z' \subseteq Z$ is *absorbing* if once the ($\epsilon = 0$) deterministic dynamic enters the set it will not leave it and if it is minimal in the sense that it has no proper subset satisfying this property. We are interested in absorbing sets in which play settles down to a stationary distribution. Let $P_{zz'}$ denote the probability of transition from state z to state z' . Let A be an absorbing set of the model without noise. The *basin of attraction* of A , denoted by $D(A)$, is the set of all states from which the unperturbed Markov process converges to a state in A . The characterization of the long-run predictions of the stochastic model will rely on the calculation of two useful concepts capturing the relative persistence over time of various absorbing sets: the *radius* and the *coradius* of their respective basins of attraction (see Ellison, 2000). While the formalization of these concepts requires the use of some additional mathematical notation (see SI Appendix), they are intuitive to grasp. Suppose the system is in an absorbing set A . The *radius* of the basin of attraction of A corresponds to the minimum number of mutations neces-

sary to leave the basin of attraction. Next, compute the minimum number of mutations needed to reach the basin of attraction of A , starting from an absorbing set outside A . Do the same for all other absorbing sets outside A , and determine the maximum of these numbers. This number is the *coradius* of the basin of attraction of A . The smaller the coradius, the likelier is the event that simultaneous mutations shift the system from any absorbing state to some state in $D(A)$. Ellison (2000) derived a sufficient condition for an absorbing set to be uniquely selected by the stochastic evolutionary process as the mutation rate vanishes: if the radius of the basin of attraction of an absorbing set A is larger than its coradius, all stochastically stable sets are contained in A .

Intuitively, the radius provides a bound on the persistence of a set, while the coradius provides a bound on its attractiveness. When $R(A) > CR(A)$ all stochastically stable outcomes are in A . We will make use of the following concept that is related to the coradius. The *modified coradius*, $CR^*(A)$ captures the insight that, under certain conditions, large evolutionary changes might occur more rapidly via a sequence of gradual steps through a number of "transient" steady states; see Ellison (2000). The modified coradius is most useful in models with a large number of deterministic steady states. It is computed by subtracting from the coradius a correction term which depends on the number of intermediate steady states along the evolutionary path and on the sizes of their basins of attraction. When $\epsilon > 0$, the invariant distribution $\mu(\epsilon)$ exists and is globally stable (see SI Appendix). In addition, for (almost all) histories of sufficient length, the weight a state receives in the invariant distribution corresponds to the fraction of time the system spends in this state (ergodicity). More formally, define the limit distribution by $\mu^* = \lim_{\epsilon \rightarrow 0} \mu(\epsilon)$. The *stochastically stable set* is defined by $Z^* = \{z \in Z : \mu^*(z) > 0\}$. Define $\mu^*(A) = \sum_{z \in A} \mu^*(z)$ with $\mu^*(Z^*) = 1$. For any absorbing set A , if $R(A) > CR^*(A)$, then $\mu^*(A) = 1$.

In short, the introduction of noise (mutations) allows us to make sharp predictions about the long-run behavior of a dynamical system whose deterministic version involves multiple steady states. Furthermore, as long as the dynamical system satisfies the weak monotonicity (Darwinian) property, its details regarding speed of adjustment do not matter. Its long-run behavior is determined by the stochastic mutations. These allow for multiple transitions across different steady states. However, in the long-run, the steady state equilibrium with the largest basin of attraction is played "most of the time." The independence of the theoretical predictions on the details of the payoff

matrix and those of the dynamical system involved is a desirable property since these factors are unlikely to remain constant over evolutionary time horizons.

An example picture of the dynamics is shown in Figure 3. The states 0 and $n = 12$ refer to the two pure strategy Nash equilibria corresponding to mycorrhizal fungi mutualisms (**AM**) and complete abandonment (**NM**). The three intermediary states in blue correspond to (mixed) Nash equilibria, reflecting different levels of partial mycorrhizal fungi mutualisms (**AMNM**).

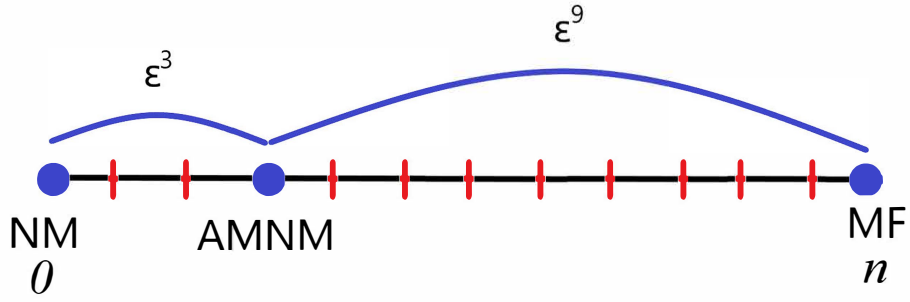


Figure 3: Coordination game: stochastic dynamics

It is worth pointing out some qualitative features of the implied dynamics using the illustrative example in Figure 3. First, all five circled states in Figure 3, corresponding to the two pure (**AM** and **NM**) and the three mixed (**AMNM**) Nash equilibria in this example, are steady states of the dynamical system $z_{t+1} = b(z_t)$ discussed earlier. Second, when random mutations are introduced, the resulting Markov chain implies a positive probability of transition from any state in $Z = \{0, 1, \dots, 12\}$ to any other. As states that do not correspond to deterministic steady states are transient, in determining the support of the invariant distribution it is sufficient to consider the steady states, associated with the pure and mixed Nash equilibria. In the above illustrative example, it takes a minimum of seven mutations to escape the basin of attraction of the **AM** steady state, an event that takes an expected time of $\frac{1}{\epsilon^7}$. Similarly, escaping the basin of attraction of the **NM** steady state requires a minimum of three mutations, an event that takes an expected time

of $\frac{1}{\epsilon^3}$. Finally, as the basin of attraction of either of the mixed steady states is a singleton, escaping either of them requires a single mutation, an event that takes an expected time of $\frac{1}{\epsilon}$. When the mutation rate, ϵ , is small, these expected times have sharp predictions about the fraction of time that the system spends at each state over a long enough history. More precisely, in the above example the set of absorbing states is $Z' = \{0, 3, 4, 5, 12\}$, where only states $z = 0$ and $z = 12$ have a non-trivial basin of attraction. We can then compute that $R(12) = 7 > 4 = CR^*(12)$, while $R(0) = 3 < 8 = CR^*(0)$. Thus, under sufficiently low mutation rates, state $z = 12$, corresponding to the **AM** Nash equilibrium, would be observed most frequently over a large time horizon. The use of modified co-radius tightens the bounds by capturing the fact that the **AM** state is more likely to be reached through intermediary **AMNM** states, a prediction that is consistent with the evolutionary record.

It is also worth reiterating that these predictions follow directly from the coordination structure of the underlying game and they do not depend on the specific details of the dynamical system or the payoff matrix, which would be very hard to infer in most applications. Of course, relative payoffs are relevant, as they determine the relative size of the basins of attraction of the various absorbing sets. Thus, the model is consistent with the observation that a reduction in the benefit-to-cost ratio of the mutualism contributes to the probability of mutualism abandonment. The biological explanation is that this is because a reduced benefit-to-cost ratio of the symbiosis should result in stronger natural selection to limit root colonization. The mathematical explanation provided by our model is that a reduction in the mutualism benefit-to-cost ratio reduces the size of the basin of attraction of the **AM** absorbing set, thus requiring a smaller number of mutations for the system to escape to an **AMNM** state.

4 Quantitative explorations

We will illustrate some of our main findings through a few representative simulations of the basic model using the replicator dynamic, $B(z)$ in (9). In principle, the model can be calibrated using phylogeny data to obtain information about the respective basins of attraction of the three types of Nash equilibria. For example, Maherali et al, 2016 calculated 4.23 transitions per million years from the **AMNM** to the **AM** state per (see Figure 1). This amounts to approximately one such transition per 236,407 years or, if we set a

period to equal 10 years, to approximately one transition per 23,600 periods. With a slight abuse in notation we now let $z \in [0, 1]$ stand for the fraction of players playing s_1 (the two pure Nash equilibria are then given by $z = 0$ and $z = 1$, respectively). Our theoretical model implies that the expected time before such a transition is $\frac{1}{\epsilon z^* n}$ periods. Given ϵ and n the equation $\frac{1}{\epsilon z^* n} = 23,600$ can thus be solved for the basin of attraction of the **AM** Nash equilibrium, $z^* n = \ln(\frac{1}{23,600} - \epsilon)$. Similarly 0.054 transitions from the **AMNM** to the **NM** state per million years (see Figure 1), imply (assuming again that a period equals 10 years) that the basin of attraction of the **NM** Nash equilibrium is given by $(1 - z_*)n = \ln(\frac{1}{1,851,852} - \epsilon)$. Given the horizons involved, such transitions are, of course, far too infrequent. We will thus simulate a stylized numerical example in what follows in order to illustrate some features of the model.

We divide the state space into three regions. For the simulations we need to pick the number of players, n , the mutation rate, ϵ , and the time horizon, T , as well as the initial condition, $z_0 \in [0, 1]$. We chose $n = 50$, $\epsilon = .2$, and $T = 600$. In addition, we chose the indifference (mixed strategy) region to be between $z_* = 0.2$ and $z^* = 0.7$. The initial condition z_0 was chosen randomly according to a uniform distribution across the (discretized) state space. The precise payoffs used in the simulations are given in the SI Appendix. Recall that it is only the difference in payoff sign that matters for the long-run model predictions. The graphs in Figure 4 present representative results from four different simulations. In all four graphs the horizontal axis measures time $t = 1, \dots, 600$, while the vertical axis represents the fraction of players choosing strategy s_1 (**AM**). Thus, $z_t = 1$ represents the **AM** equilibrium, $z_t = 0$ represents the **NM** equilibrium, while the region between the two horizontal lines, $z_t \in [0.2, 0.7]$, represents the mixed strategy Nash equilibrium points (**AMNM**). The coordination structure of the game implies that the basin of attraction of the **AM** equilibrium is given by the interval $[0.7, 1]$, while the basin of attraction of the **NM** equilibrium is the interval $[0, 0.2]$. This makes the **AM** equilibrium the one selected to be played “most of the time” over a sufficiently long time horizon.

The first graph (top left) in Figure 4 represents a simulation where the system stays in the basin of attraction of the **NM** Nash equilibrium. Ongoing *iid* mutations perturb the system away from $z = 0$, but they do not arise in sufficient magnitude over the simulation horizon to create the market thickness that is necessary for the system to establish a (partial or full)

mutualism. Similarly, the second graph (top right) represents a simulation where the system stays in the basin of attraction of the **AM** Nash equilibrium. Again, ongoing *iid* mutations perturb the system away from $z = 1$, but they are not sufficient for the system to escape the basin of attraction of the symbiotic Nash outcome, and the mutualism remains more or less intact for the duration.

More interestingly, the simulation in the third graph (bottom left) involves a transition away from the basin of attraction of the **NM** equilibrium, leading to an eventual emergence of the symbiotic **AM** Nash outcome. Consistent with the historical record in Maherali et al (2016), the transition occurs when a sufficient number of mutations move the system out of the basin of attraction of the **NM** Nash equilibrium and in the mixed **AMNM** region, where the system spends some time (6.3% of the simulation time horizon) before it enters the basin of attraction of the **AM** Nash equilibrium, where it stays for the duration of the simulation. Of course, we know from our theoretical results that several transitions would be observed over a sufficiently long time horizon. However, these results also imply that the system will spend the majority of time around the **AM** Nash equilibrium.

The mutations constantly perturb the system away from the Nash outcomes, but most of the time they are too small in magnitude to sufficiently increase/reduce market thickness, and evolutionary forces return the system towards the corresponding Nash equilibrium. Occasionally, a large number of mutations lead to a significant reduction/increase in market thickness, and a corresponding reduction/increase in the fitness of the symbiotic strategy. This is sufficient for the system to escape the basin of attraction of the corresponding Nash outcome. The simulation in the fourth graph (bottom right) involves the system starting in the basin of attraction of the **AM** equilibrium, then entering the basin of attraction of the **NM** Nash outcome through the mixed **AMNM** region, and finally switching back to the **AM** outcome for the remaining duration of the simulation. Again, consistent with the historical record, these transitions occur through intermediary **AMNM** states, with the system spending some time (8.2% of the simulation horizon) in the intermediary **AMNM** mixed strategy Nash region. Of course, should the simulation horizon increase, several (infrequent) transitions across the Nash equilibria will be observed, leading to the long-run weights of the respective Nash equilibria prescribed by the ergodic distribution μ .

Maherali et al (2016) have pointed out that environmental and other changes that reduce the benefit-to-cost ratio associated with the symbiosis

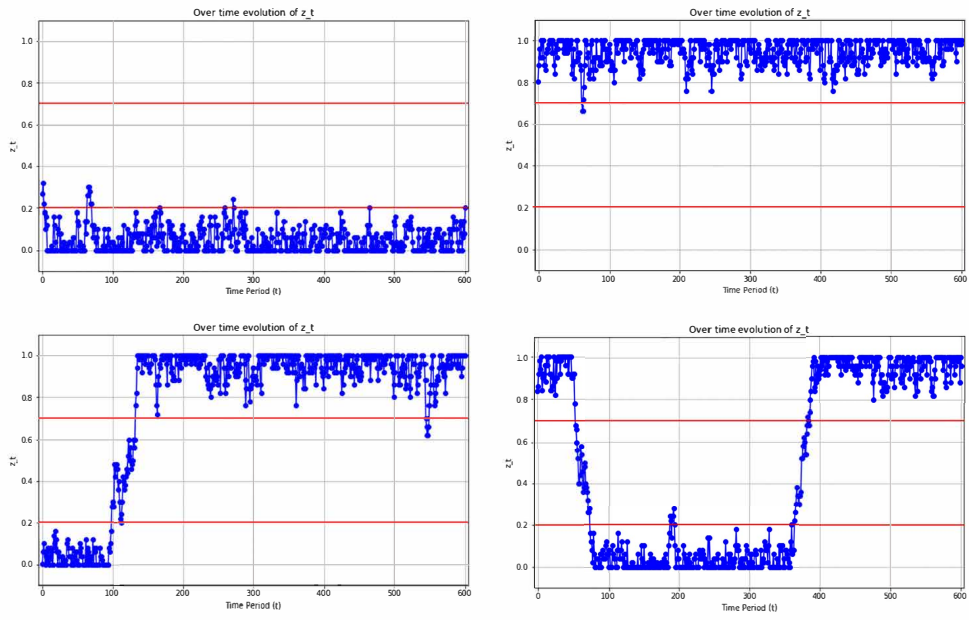


Figure 4: Coordination game simulated play

increase the likelihood of its abandonment. This insight is confirmed in the context of the coordination game we study here since the change in the game's payoffs resulting from a reduction in the benefit-to-cost ratio would lead to a smaller basin of attraction of the **AM** Nash equilibrium and a correspondingly larger basin of attraction of the **NM** Nash equilibrium. As an example, below we represent the results from representative simulations under the same conditions as before, but with the basin of attraction of the **AM** equilibrium now given by the smaller interval $[0.8, 1]$, while the basin of attraction of the **NM** equilibrium is the larger interval $[0, 0.4]$.

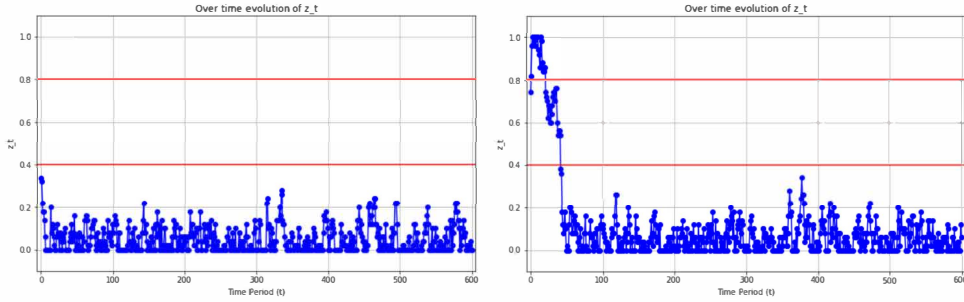


Figure 5: Lower symbiosis benefit/cost ratio

Regardless of the initial condition, over a long time horizon play in this case concentrates around the **NM** Nash equilibrium (Figure 5, left). Once again, play moves repeatedly along the different basins of attraction over evolutionary time. If the initial state is within the basin of attraction of the **AM** Nash equilibrium, play will concentrate there for a number of periods. However, as the basin of attraction of this equilibrium shrinks, it becomes easier to escape, leading to a transition (usually indirectly through the **AMNM** steady states) towards the **NM** equilibrium, where the system will spend a long time before it eventually escapes again. Of course, the reverse conclusion would be reached if the benefit-to-cost ratio associated with the symbiosis was to increase. In that case, an increase in the size of the basin of attraction of the **AM** Nash equilibrium would make it the preferred outcome over a long time horizon.

5 Conclusions

We employed techniques from large deviation theory to study stochastic evolutionary dynamics in the context of a biological market. The coordination game structure allowed us to build a rigorous theory of mutualism emergence and abandonment that emphasizes the benefits of the biological market size and does not rely on the possibility of “cheating” among participants. We illustrated our results in the context of the seed plant-mycorrhizal fungi mutualism. Our model captured some of the main findings in the formal ancestral reconstruction in seed plants in Maherali et al (2016). Notably, our findings are consistent with the observation that the mutualism has been abandoned and re-established several times through evolutionary time, but it is more likely to persist than be abandoned. We found that, while the symbiosis emergence and abandonment could occur via direct transitions between the **AM** and the **NM** states, they are far more likely to occur via an intermediate reversion through mixed **AMNM** states. Over a long enough time horizon, the system spends most of the time in the Nash equilibrium with the largest basin of attraction (**AM**). However, the system will eventually escape and reach another absorbing set before it escapes again over long evolutionary time horizons. Since exploitation of plants by mycorrhizal fungi appears to be infrequent (Maherali et al. 2016), we treated the fungi as passive in our analysis and concentrated on the interactions among host plants, as in Halloway et al (2022). A more general analysis would involve both sides of this biological market playing an asymmetric coordination game. The application of the modified co-radius formalizes the notion that large evolutionary changes are more likely when they can be achieved by passing through a number of “transient” steady states. In this context, it explains why the **AM** state is reached more frequently through the intermediary state (**AMNM**). A consequence of the multiple Nash equilibrium coordination game framework is that the **AM**-plant mutualism might be (partially or fully) abandoned by the plants even if it is overall superior for plant fitness. Thus, coordination games giving rise to multiple, Pareto-ranked, Nash equilibria might provide a rationale for why evolution can get stuck in “local fitness maxima,” while global maxima might coexist. This can have applications in other biological contexts.

CODE. The code used in our simulations can be found at:

GitHub: <https://github.com/hemitheo/Mutualisms>

FUNDING INFORMATION. No outside funding was used in this research.

ACKNOWLEDGMENTS. Corresponding author: Ted Loch-Temzelides. We thank participants at the 2025 Mathematics of Uncertain Systems conference in Rimini, Italy the 16th Conference on Optimal Control and Dynamic Games in Vienna, Austria, and the AI, Data, and Decision Sciences Department at LUISS University (Rome, Italy) for comments. Pierre Loch provided computational assistance.

6 References

- Archetti, M., Scheuring, I., Hoffman, M., Frederickson, M. E., Pierce, N. E., & Yu, D. W. (2011). Economic game theory for mutualism and cooperation. *Ecology letters*, 14(12), 1300-1312.
- Baker, A. Reef corals bleach to survive change. *Nature* 411, 765–766 (2001). <https://doi.org/10.1038/35081151>
- Blume, Andreas, and Ted Temzelides. On the geography of conventions. *Economic Theory* 22: 863-873 (2003)
- Bronstein, Judith L. The exploitation of mutualisms. *Ecology letters* 4.3 (2001)
- Bronstein, Judith L., Ruben Alarcón, and Monica Geber. The evolution of plant–insect mutualisms. *New Phytologist* 172.3: 412-428 (2006)
- Boulotte, N., Dalton, S., Carroll, A. et al. Exploring the Symbiodinium rare biosphere provides evidence for symbiont switching in reef-building corals. *ISME J* 10, 2693–2701 (2016). <https://doi.org/10.1038/ismej.2016.54>
- Culley, T. M., S. G. Weller, and A. K. Sakai. The evolution of wind pollination in angiosperms. *Trends in Ecology and Evolution* 17:361–369 (2002)
- Dembo, Amir, and Ofer Zeitouni. *Large deviations techniques and applications*. Stochastic Modelling and Applied Probability Vol. 38. Springer Science & Business Media (2009)

- Ellison, G.: Basins of attraction, long run equilibria, and the speed of step-by-step evolution. *Review of Economic Studies* 67 (1), 17-45 (2000)
- Ferriere, Régis, et al. Cheating and the evolutionary stability of mutualisms. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 269.1493: 773-780 (2002)
- Freidlin M. I., Wentzell A. D.: *Random perturbations of dynamical systems*. 1st Edition, New York: Springer Verlag (1984)
- Friedman, J. Gone with the wind: understanding evolutionary transitions between wind and animal pollination in the angiosperms. *New Phytologist* 191:911–913 (2011)
- Fudenberg D., Levine D.K.: *The theory of learning in games*. Cambridge, MA: MIT Press (1998)
- Halloway, Abdel H., Katy D. Heath, and Gordon G. McNickle. When does mutualism offer a competitive advantage? A game-theoretic analysis of host–host competition in mutualism. *AoB Plants* 14.2 (2022)
- Jones, Emily I., et al. Cheaters must prosper: reconciling theoretical and empirical perspectives on cheating in mutualism. *Ecology letters* 18.11: 1270-1284 (2015)
- Josef Hofbauer and Karl Sigmund, *Evolutionary Games and Population Dynamics*, Cambridge University Press (1998)
- Kandori, M., Mailath, G., Rob, R.: Learning, mutation, and long run equilibria in games. *Econometrica* 61 29-56 (1993)
- Kauffman, S. and Levin, S.. Towards a general theory of adaptive walks on rugged landscapes. *Journal of theoretical Biology*, 128(1), pp.11-45 (1987)
- Levin, J., Miller, J. Broadband neural encoding in the cricket cereal sensory system enhanced by stochastic resonance. *Nature* 380, 165–168 (1996)
- Maherali, Hafiz, Brad Oberle, Peter F. Stevens, William K. Cornwell, and Daniel J. McGlinn. Mutualism persistence and abandonment during the evolution of the mycorrhizal symbiosis. *The American Naturalist* 188, no. 5: E113-E125 (2016)

- McNickle, Gordon G., and Ray Dybzinski. Game theory and plant ecology. *Ecology letters* 16, no. 4: 545-555 (2013)
- Nash, J. F. Non-cooperative games: *The Annals of Mathematics*, v. 54: 286-295 (1951)
- Noë, R., & Hammerstein, P. (1994). Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral ecology and sociobiology*, 35, 1-11
- Noë, R, and P. Hammerstein. Biological markets, *Trends in Ecology & Evolution*, Volume 10, Issue 8, Pages 336-339, [https://doi.org/10.1016/S0169-5347\(00\)89123-5](https://doi.org/10.1016/S0169-5347(00)89123-5) (1995)
- John Maynard Smith, *Evolution and the Theory of Games*, Cambridge University Press (1982)
- Palmer, Todd M., Maureen L. Stanton, Truman P. Young, Jacob R. Goheen, Robert M. Pringle, and Richard Karban. “Breakdown of an Ant-Plant Mutualism Follows the Loss of Large Herbivores from an African Savanna.” *Science* 319, no. 5860 (2008): 192–95. <http://www.jstor.org/stable/20051975>
- Palmer, Todd M., Maureen L. Stanton, Truman P. Young, John S. Lemboi, Jacob R. Goheen, and Robert M. Pringle. A Role for Indirect Facilitation in Maintaining Diversity in a Guild of African Acacia Ants. *Ecology* 94, no. 7: 1531–39 (2013). <http://www.jstor.org/stable/23596942>
- Taylor P.D. and L.B. Jonker, Evolutionarily Stable Strategies and Game Dynamics, *Mathematical Biosciences*, 40(1–2), 145–156 (1978)
- Vasconcelos, Vítor V, Constantino, Sara M, Dannenberg, Astrid, Lumkowsky, Marcel, Weber, Elke, Levin, Simon: Segregation and clustering of preferences erode socially beneficial coordination. *Proceedings of the National Academy of Sciences* 118(50) (2021)
- Werner, G. D., W. K. Cornwell, J. I. Sprent, J. Kattge, and E. T. Kiers. A single evolutionary innovation drives the deep evolution of symbiotic N₂-fixation in angiosperms. *Nature Communications* 5:4087 (2014)

- Werner, G. D., J. H. C. Cornelissen, W. K. Cornwell, N. A. Soudzilovskaia, J. Kattge, S. A. West, and E. T. Kiers, Symbiont switching and alternative resource acquisition strategies drive mutualism breakdown, *Proceedings of the National Academy of Sciences*, vol. 115 no. 20, 5229–5234 (2018)
- Xu, Li, Denis Patterson, Ann Carla Staver, Simon Asher Levin, and Jin Wang. Unifying deterministic and stochastic ecological dynamics via a landscape-flux approach. *Proceedings of the National Academy of Sciences* 118, no. 24 (2021): e2103779118
- Xu, L., Patterson, D., Levin, S.A. and Wang, J. Non-equilibrium early-warning signals for critical transitions in ecological systems. *Proceedings of the National Academy of Sciences*, 120(5), p.e2218663120 (2023)
- Young, P. H.: The evolution of conventions. *Econometrica* 61, 57-84 (1993)

7 Supplemental information

7.1 Stochastic evolutionary dynamics

Introducing noise or mutations turns the deterministic dynamical system, $z_{t+1} = b(z_t)$, into a stochastic dynamical system:

$$z_{t+1} = b(z_t) + z_{1t} - z_{2t} \quad (10)$$

where z_{1t} , z_{2t} follow binomial distributions: $z_{1t} \sim B(n - b(z_t), \epsilon/2)$, and $z_{2t} \sim B(b(z_t), \epsilon/2)$. The stochastic dynamical system gives rise to a Markov chain with transition matrix:

$$P = [z_{t+1} = j | z_t = i] \quad (11)$$

where $i, j = 0, \dots, n$. Let $\mu(\epsilon)$ be an *invariant distribution* associated with P ; i.e., $\mu(\epsilon)P = \mu(\epsilon)$. Since $\epsilon > 0$, every element of P is strictly positive. As is well known, this is a sufficient condition for the existence and uniqueness of $\mu(\epsilon)$. In addition, μ satisfies the following properties:

Global stability: $\forall \mu_0, \lim_{t \rightarrow \infty} \mu_0 P^t \rightarrow \mu$

Ergodicity: Define:

$$I_i(z_t) := \begin{cases} 1, & \text{if } z_t = i \\ 0, & \text{if } z_t \neq i \end{cases}$$

Then, $\forall z_0, \lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=1}^T I_i(z_t) \rightarrow \mu_i$ almost surely.

Define the limit distribution by $\mu^* = \lim_{\epsilon \rightarrow 0} \mu(\epsilon)$. The *stochastically stable set* is defined by $Z^* = \{z \in Z : \mu^*(z) > 0\}$. Let $\mu^*(A) = \sum_{z \in A} \mu^*(z)$ with $\mu^*(Z^*) = 1$. We next discuss characterizing the invariant distribution. First, we have the following notion for long-run outcomes of the deterministic ($\epsilon = 0$) dynamic, $b(z)$.

Definition 3: A set of states $Z' \subseteq Z$ is absorbing if (i) for all $z' \in Z'$, $z \notin Z'$, $P_{z'z} = 0$, and (ii) $\nexists Z'' \subset Z'$, $Z'' \neq Z'$ s.t. (i) holds for Z'' .

The first condition requires that once the process enters the absorbing set, it will not leave it. The second condition requires that absorbing sets are minimal. We are interested in absorbing sets in which play settles down to a stationary distribution. Let $P_{zz'}$ denote the probability of transition from state z to state z' . Let A be an absorbing set of the model without noise. The *basin of attraction* of A , denoted by $D(A)$, is the set of all states from which the unperturbed Markov process converges to a state in A with probability one,

$$D(A) = \{z \in Z | \Pr(\exists \tau' \text{ s.t. } z_\tau \in A \forall \tau > \tau' | z_0 = z) = 1\} \quad (12)$$

For any set A , the *radius* of $D(A)$, is the number of mutations necessary to leave the set, starting from a state in A (see Ellison, 2000). Let $c(z, z')$ be the number of mutations needed for the system to transit from state z to state z' . That is, $c(\cdot)$ measures the *transition cost* between these states. Define a *path* by a finite sequence $(z_1, \dots, z_k)$ of distinct states. The *cost* of such a path is defined by

$$c(z_1, \dots, z_k) = \sum_{\tau=1}^{k-1} c(z_\tau, z_{\tau+1}) \quad (13)$$

Formally, the *radius* of A is the least costly path leading from any state in A to some state outside the basin of attraction of A .

Definition 4: The *radius of the basin of attraction of a collection of absorbing sets A* is

$$R(A) = \min_{(z_1, \dots, z_k)} c(z_1, z_2, \dots, z_k) \text{ s.t. } z_1 \in A, z_k \notin D(A) \quad (14)$$

The path $(z_1, \dots, z_k)$ defining the radius of $D(A)$ describes the “cheapest” way out of that set. Formally, the *coradius* of the basin of attraction of a

collection of absorbing sets is defined by the number of mutations necessary to reach this set from the state where the minimum number of mutations required to reach $D(A)$ is maximized.

Definition 5: *The coradius of the basin of attraction of a set of absorbing sets A is: $CR(A) = \max_{z_1 \notin A} \min_{(z_1, \dots, z_k)} c(z_1, \dots, z_k)$ such that $z_k \in D(A)$.*

When $R(A) > CR(A)$ all stochastically stable sets are in A and that the expected waiting time until a limit set A is reached is at most $O(\epsilon^{-CR(A)})$ (see Ellison, 2000).

Definition 6: *The modified coradius of the basin of attraction of a collection of absorbing sets A is given by:*

$$CR^*(A) = \max_{z^1 \notin A} \min_{(z^1, \dots, z^k)} \{c(z_1, \dots, z_k) - \sum_{l=2}^{L-1} R(Z_l)\} \text{ s.t. } z_k \in D(A) \quad (15)$$

where $\{Z_l\}$ is the sequence of absorbing sets through which $(z_1, \dots, z_k)$ passes.

A tighter bound on the expected waiting time until a limit set A is reached is then at most $O(\epsilon^{-CR^*(A)})$. A sufficient condition for a set of states to be stochastically stable is that the radius of its basin of attraction exceeds the modified coradius. We restrict attention to such states. When $R(A) > CR^*(A)$ all stochastically stable sets are in A and that the expected waiting time until a limit set A is reached is at most $O(\epsilon^{-CR^*(A)})$ (see Ellison, 2000).

7.2 Sketch of the algorithm steps used in simulations

Fix number of players: n

Fix mutation rate: ϵ

Fix number of periods: $t = 0, \dots, T$

Fix initial condition: $z_0 = \text{random fraction in } [0, 1]$

Define fraction of s_1 players at t : $z_t \in [0, 1]$

Define fraction of s_2 players at t : $1 - z_t$

Define payoff from playing s_1 at t : $u(s_1, z_t)$

Define payoff from playing s_2 at t : $u(s_2, z_t)$

Set $u_t(z_t) := (s_1, z_t) - u(s_2, z_t)$ where, for all t ,

$$u(z_t) := \begin{cases} -1, & \text{if } z_t < z_* \\ 0, & \text{if } z_t \in [z_*, z_*] \\ +1, & \text{if } z_t > z^* \end{cases}$$

For all t , set: $u(s_1, z_t) := \begin{cases} 2, & \text{if } z_t < z_* \\ 2.5, & \text{if } z_t \in [z_*, z_*] \\ 3, & \text{if } z_t > z^* \end{cases}$, $u(s_2, z_t) := \begin{cases} 3, & \text{if } z_t < z_* \\ 2.5, & \text{if } z_t \in [z_*, z_*] \\ 2, & \text{if } z_t > z^* \end{cases}$

$$z_{t+1} = z_t \left[\frac{u(s_1, z_t)}{z_t u(s_1, z_t) + (n - z_t) u(s_2, z_t)} \right] + \epsilon(1 - z_t) - \epsilon z_t \quad (16)$$

Starting with z_0 , use the iterative process above to compute z_t for every integer time period t , $t = 0, \dots, T$

Compute the fraction of time the system spends in each region R_1, R_2, R_3

Compute the fraction of transitions from $z = 1$ to $z = 0$ that occurred directly, versus through $z \in [z_*, z^*]$