Evolutionary games with environmental feedbacks

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Abstract

Strategic interactions often occur in dynamic environments that change according to the behavior of individuals. Feedback between the environment and individual behavior is common in social-ecological systems, evolutionary-ecological systems, and even psychological-economic systems – where the state of the environment alters the dynamics of competing strategies or types, and vice versa. When feedbacks are present, the dynamics of strategies and resources must be considered jointly: neither alone can describe the dynamics of the system. Here we develop a framework for eco-evolutionary game theory that permits the study of strategic dynamics with environmental feedbacks. We provide a complete dynamical analysis for two-strategy games with environmentally dependent payoffs, where the environment is impacted by the strategies employed. The environment in these systems may be governed either as a renewable resource (e.g. common-pool harvesting) or as a decaying resource (e.g. pollution byproducts). We find that for many regimes, despite feedbacks, persistent dynamical cycles are not possible. In regimes where cycling is possible, cycles occur only when the timescale of environmental change is sufficiently slow compared to the timescale of strategic change. We show that a number of prior studies on joint strategic-environmental dynamics, across a range of disciplines, can be understood as special cases of our general analysis. We discuss the implication of our results for fields ranging from ecology to economics.

In many interactions an individual's payoff depends on both her own strategy or type, as well as the strategic composition in the entire population. Such interactions arise across a range of disciplines, from microeconomics to the evolution of animal behavior, and they have been analyzed using game theory (Nash, 1950; Smith, 1982). However, game-theoretic analysis of competing types typically assumes that the form of strategic interaction is either fixed in time, or depends on an independent exogenous environment. Real-world systems, however, often feature bi-directional feedbacks between the environment and the nature of strategic interactions: an individual's payoff depends not only her actions relative to the

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population, but also on the state of the environment, and the state of the environment is influenced by the actions adopted by all individuals in the population.

Strategic-environmental feedbacks are commonplace in social-ecological systems. In a fishery, for example, the relative reward of a high-intensity versus a low-intensity harvesting strategy depends upon the current biomass of the fish stock; and, conversely, stock dynamics depend on the frequencies of these two harvesting strategies. When the fish stock is high, firms employing the high-intensity harvesting will tend to outcompete low-intensity firms, but also deplete the stock. But when the stock is low, low-intensity firms will tend to increase in frequency (because they avoid wasted effort) and consequently allow the fish stock to rebound. One might naturally expect a cyclical dynamic to emerge, with periods of high-intensity harvesting strategies dominating when stock biomass is large, followed by low-intensity firms dominating during periods of low stock biomass, and so on. The joint dynamics of the strategies of harvesters and the state of the environment constitute social-ecological feedback system. Here we develop a framework to study such systems as eco-evolutionary games.

Reciprocal feedbacks between strategic interactions and the environment play out in many complex systems with broad biological and societal relevance. For example, dynamical linkages between social and ecological processes can produce multiple stable states and complex dynamics (Sethi and Somanathan, 1996; Tavoni et al., 2012; Levin et al., 2013; Tilman et al., 2017, 2018; Mullon et al., 2018). In ecology, species strategies and interactions determine the competitive balance among species whilst also changing their environment and, in turn, the nature of competition. For example, symbiotic nitrogen fixation in plants increases local nitrogen availability through time, thus altering the competitive environment (Menge et al., 2008). Likewise, global climate change is caused by the strategic decisions of individuals, corporations, and nations, which have long-timescale environmental repercussions that in turn will alter the strategic landscape those parties face. In psychology, deliberative decision-making can beneficially shape the shared environment of social norms and institutions, but that environment then sets the stage for the success of less costly, non-deliberative decision-making (Rand et al., 2017). Examples from these diverse fields share the common thread that feedbacks between strategies and the environment fundamentally alter dynamical predictions (Stewart and Plotkin, 2014; Weitz et al., 2016; Akçay, 2018; Cortez et al., 2018). Better understanding of such systems requires a general framework for studying strategic dynamics when the nature of competitive interactions influences the environment, and conversely.

Of particular interest are feedbacks between the strategies in a population and the payoff structures that determine the further evolution of these strategies. Such feedbacks can arise

when evolutionary and ecological dynamics occur on similar timescales (Cortez and Ellner, 2010). Several studies have considered the evolutionary consequences of new strategies being added to a game (Worden and Levin, 2007; Huang et al., 2012), or of mutations that change the payoffs from existing strategies (Akçay and Roughgarden, 2011; Stewart and Plotkin, 2014). Other work explores how dynamics change when the strategies being played in a population (Peck and Feldman, 1986) or in a social interaction (Hilbe et al., 2018) directly alter the payoff structure of future interactions. Here, we focus on the general problem in which strategies adopted in a population of players alter the dynamics of an environmental resource, which in turn alters the payoffs to different strategies (Weitz et al., 2016; Rand et al., 2017).

We develop a general, unifying framework for eco-evolutionary games and perform a detailed analysis of an arbitrary two-strategy game bi-directionally linked to a renewable or decaying resource. We show that many of the socio-environmental systems studied in the literature are special cases of our general model – which allows us to draw general conclusions about socio-environmental dynamics. We derive stability criteria for all strategic/environmental equilibria, and we derive the conditions that permit cyclic dynamics, bistability, or a stable interior equilibrium. Our key finding is that system dynamical behavior depends critically on the timescale separation between strategy and environmental dynamics.

Our framework encompasses many previously studied systems as special cases, including common-pool resource harvesting, controlled versus automatic processing in human cognition, and grass-legume competition with nitrogen feedbacks. We also extend our framework of common-pool resource harvesting to account for market pricing or frequency-dependent harvesting efficiency. We find that cycles arise only in a restricted subset of game structures that exclude standard models of common-pool resource harvesting. More generally, we show that environmental feedbacks alter equilibrium outcomes reached and expand the suite of dynamical possibilities for a system, and that we can characterize their dynamical behavior in terms of a few easily interpretable quantities.

1 Eco-evolutionary games

We describe a general framework for coupled environmental and strategic dynamics. We consider a population with agents who choose strategies from a set S of K strategies, each with an associated environmental impact. We assume that the fitness of a strategy $j \in S$ is $\pi_j(\mathbf{x}, n)$ where fitness is a function of the the state of the environment, n, and the frequencies of strategies currently employed in the population, $\mathbf{x} = [x_1, x_2, \ldots, x_K]$, which we call the

population strategy profile. We let the strategy profile of the population evolve according to the replicator equation (Taylor and Jonker, 1978),

$$\dot{x}_i = \epsilon_3 x_i \left(\pi_i(\mathbf{x}, n) - \phi(\mathbf{x})\right) \tag{1}$$

where the mean fitness of the population is $\phi(\mathbf{x}) = \sum_{j=1}^{K} x_j \pi_j(\mathbf{x}, n)$, and ϵ_3 is a parameter that determines the speed of strategy dynamics.

Next we describe environmental feedbacks. Each strategy has an impact on the environment channeled through a function, $h(\mathbf{x}, n)$, that aggregates the impact of the current population strategy profile, and which may depend on the current state of the environment. The environment n also has its own intrinsic dynamics that occur in the absence of interference, governed by $f(n)$, so the overall dynamics take the form

$$\dot{n} = \epsilon_1 f(n) - \epsilon_2 h(\mathbf{x}, n) \,, \tag{2}$$

where ϵ_1 and ϵ_2 determine the speeds of the intrinsic environmental dynamics (independent of strategies played) and of the extrinsic impact of strategies on the environment, respectively. In total, we have a system of K differential equations (1 environmental equation and $K-1$ strategy equations, since $\mathbf{x}$ lies on a simplex). For a two-strategy game we can simplify our system to

$$\dot{x}_1 = \epsilon_3 x_1 (1 - x_1)(\pi_1(x_1, n) - \pi_2(x_1, n)) \tag{3a}$$

$$\dot{n} = \epsilon_1 f(n) - \epsilon_2 h(x_1, n) \tag{3b}$$

because in this case $x_1 = 1 - x_2$.

This general framework features three different timescales: the timescale of intrinsic dynamics of the environment, ϵ_1, the timescale of the environmental impact of the strategies currently employed in the population, ϵ_2, and the timescale of strategy update dynamics (strategy evolution) in the population, ϵ_3. We can normalize the first two timescales relative to the third so that we drop ϵ_3, without loss of generality. This framework allows for nonlinearity in the payoff structures as well as in environmental impact and intrinsic dynamics, so that the space of models and potential dynamics is vast. We therefore focus our analysis on a subset of models where payoffs are linear in the state of the environment and the strategy frequencies.

2 Linear eco-evolutionary games

Based on our general framework, we describe a broad class of two-strategy eco-evolutionary games where the payoffs to individuals are linear in both the population strategy profile, x, and in the environmental state, $n \in (0, 1)$. Given these restrictions, we can write the payoffs in terms of the matrix

$$\Pi(n) = (1-n)\begin{bmatrix} R_0 & S_0 \\ T_0 & P_0 \end{bmatrix} + n\begin{bmatrix} R_1 & S_1 \\ T_1 & P_1 \end{bmatrix}, \tag{4}$$

where entries correspond to the payoffs of the game under conditions of lowest ($n = 0$) or highest ($n = 1$) environmental quality. Using $\Pi(n)$, we write the payoff for playing strategy 1 and strategy 2 as $\pi_1(x, n)$ and $\pi_2(x, n)$, respectively, where x is the fraction of the population that plays strategy 1. We systematically analyze games of this form coupled to resources whose intrinsic dynamics are either renewing or decaying.

2.1 Eco-evolutionary games with intrinsic resource dynamics

Intrinsic resource dynamics can take many forms. In this section, we show how different resource dynamics can be mapped onto our general framework for eco-evolutionary games. In particular, we consider two different environmental dynamics: (i) a renewable resource where each strategy exerts degradation (or harvesting) pressure on the resource stock, and (ii) a decaying resource that is produced as a by-product of each strategy.

We first suppose there is a resource stock, m, that in the absence of consumption or harvesting grows logistically, and is diminished through harvesting or consumption associated with the strategies in a game. Let e_L and e_H be the resource harvest effort of strategies L and H, respectively, with $e_L < e_H$. The resource dynamics are governed by

$$\frac{dm}{dt} = rm\left(1 - \frac{m}{k}\right) - qm\left(e_L x + e_H(1-x)\right) \tag{5}$$

where x is the fraction of the population playing strategy L, r is the intrinsic rate of resource growth, and k is the resource carrying capacity. Here q is a parameter that maps resource degradation pressures (or harvesting efforts) (e_L, e_H) into the rate of reduction in the resource. We assume that environmental impact rates are restricted so that m will be positive at equilibrium. This implies that $e_H \in (0, r/q)$ and $e_L \in [0, e_H)$.

While the resource stock m can assume any non-negative value, we map m to the environmental metric n in our framework, which is bound between 0 and 1. In particular, regardless of the initial value of m, it will eventually fall between its equilibrium values when

high- and low-effort strategies dominate the populations. Therefore, we can use a linear transformation of m that maps the equilibrium value of m when low effort resource users dominate to $n = 1$ and the equilibrium when the high effort strategy dominates to $n = 0$ (See supplementary information section S1.1).

Now, using the payoff matrix from equation 4 we can write our system as

$$\dot{x} = x(1-x)(\pi_L(x,n) - \pi_H(x,n)) \,, \tag{6a}$$

$$\dot{n} = \epsilon \left(r - q(e_L n + e_H(1-n))\right)(x-n) \,. \tag{6b}$$

In terms of our general framework (equation 2) we have $f(n) = -\left(r - q(e_L n + e_H(1-n))\right) n$ and $h(x,n) = -\left(r - q(e_L n + e_H(1-n))\right) x$. In this case, we have assumed that the timescales of intrinsic resource dynamics and resource harvesting are the same (i.e., $\epsilon_1 = \epsilon_2 = \epsilon$), so we have only one relative timescale, as opposed to two in the most general framework. In other words, ϵ quantifies the rate of environmental dynamics (both intrinsic and extrinsic) compared to the rate of strategy dynamics.

We can do a similar mapping for a model with a decaying resource, such as a pollutant. Let m denote the pollutant level in the environment now. Each strategy played in the evolutionary game produces the pollutant as a byproduct at some rate. Let e_L and e_H be the emissions rates of the low emissions and high emissions strategies, respectively. Then we can model the stock of m with the differential equation

$$\frac{dm}{dt} = -\alpha m + e_L x + e_H(1-x) \tag{7}$$

where x is the fraction of the population that plays the strategy with low emissions (strategy L), $(1-x)$ is the fraction the plays the high emission strategy and α is the decay rate of the resource stock. We can again define n as a linear transformation of m which gives $n = 1$ at the equilibrium of the resource dynamics when the whole population follows the low-emission strategy, and $n = 0$ at the corresponding equilibrium when everyone plays the high-emission strategy (see supplementary information section S2.1). This yields dynamics in n governed by

$$\dot{n} = \alpha(x-n). \tag{8}$$

Although decaying versus renewing resources stem from different biological or social phenomena, they both yield the same qualitative results and the following analysis applies to both cases.

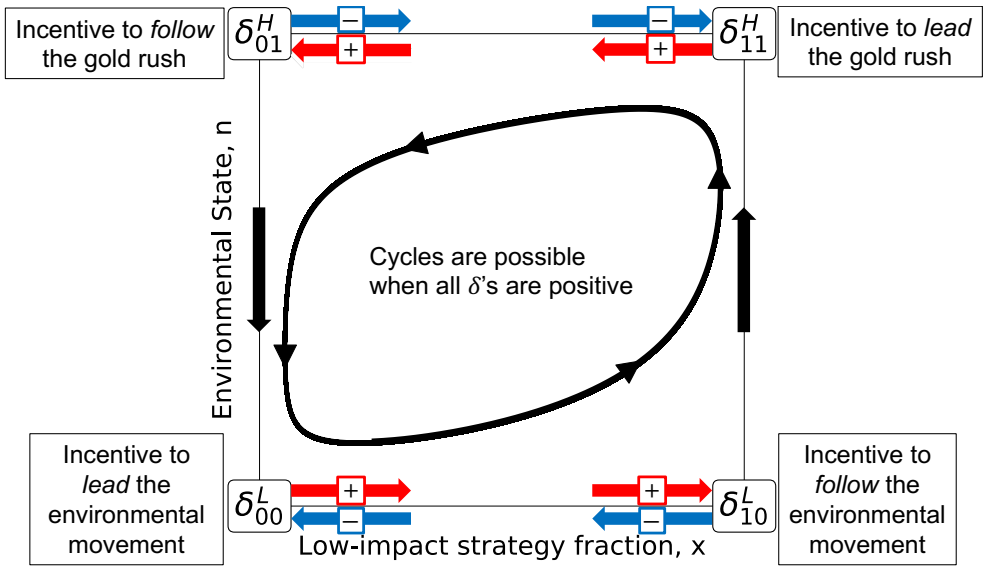


Figure 1: A graphical representation of how incentive parameters in eco-evolutionary games influence dynamics. The x-axis of the state space corresponds to the frequency of types using the strategy with low impact on the environment, where has the y-axis indicates the quality of the environment, n. Each of the four incentive parameters (δ's) controls the direction and magnitude of strategy dynamics at a corner of the state space: when a δ is positive the strategy dynamics follow the red arrows, and conversely when a δ is negative. When all δ's are positive, meaning there are incentives to lead and follow strategic changes, then some form of cyclical dynamics seem plausible because each corner exhibits saddle-like properties. However, despite this intuition, we show that all δ's being positive is neither necessary nor sufficient for cyclic dynamics in general eco-evolutionary games.

Analysis The eco-evolutionary system above depends on four parameter combinations, each which has an intuitive interpretation. We define the following parameters in terms of the payoff matrices at low-quality and high-quality environmental states:

$$\begin{aligned}
\delta_{11}^H &= \pi_H(1,1) - \pi_L(1,1) = T_1 - R_1 \\
\delta_{01}^H &= \pi_H(0,1) - \pi_L(0,1) = P_1 - S_1 \\
\delta_{10}^L &= \pi_L(1,0) - \pi_H(1,0) = R_0 - T_0 \\
\delta_{00}^L &= \pi_L(0,0) - \pi_H(0,0) = S_0 - P_0.
\end{aligned}$$

These four parameters allow us express dynamical outcomes in terms of the incentive to switch strategies when the environment is either at high or low quality. The qualitative impact of these four parameters is shown schematically in Figure 2.

The parameter δ_{11}^H quantifies the incentive to switch to the strategy with high environmental impact (denoted by the H superscript) given that all other individuals follow the low-impact strategy and the system is currently in a high environmental state ($(x = 1, n = 1)$ as denoted by the subscript 11). In the context of socio-ecological systems, δ_{11}^H can be interpreted as the incentive to *lead* a "gold rush" – that is, be the first player to switch to a high-impact strategy and reap the rewards of an abundant resource. By contrast, the parameter δ_{01}^H quantifies the incentive to switch to the high-impact strategy under a good environmental state, given that every other player has already switched. In other words, δ_{01}^H is the incentive to *follow* the gold rush.

The parameter δ_{00}^L quantifies incentive to switch to the low-impact strategy given a poor environmental state and when all other players are following the high-impact strategy. And so we can think of δ_{00}^L as the incentive to *lead* an "environmental movement" by reducing harvesting of a depleted resource. Finally, the parameter δ_{10}^L quantifies the incentive to switch to the low-impact strategy given that all other individuals are following the low-impact strategy and the environment is in a poor state. Thus δ_{10}^L can be seen as the incentive to *follow* the environmental movement.

The verbal descriptions of these four critical parameters apply in the context of socio-ecological system, such a fishery. But there are natural alternative interpretations of these parameters for a range of related phenomena across diverse fields.

The linear evo-evolutionary system has up to four equilibria. There are two edge equilibria which support a single strategy in the population, at $(x^*, n^*) \in \{(0,0), (1,1)\}$, and there are also up to two interior equilibria, which support multiple co-existing strategies in the population, denoted by (x_+^*, n_+^*) and (x_-^*, n_-^*). The edge equilibrium $(x^*, n^*) = (0,0)$ is stable only if $\delta_{00}^L < 0$, which is intuitively clear from figure 1. Similarly, the edge equilibrium

$(x^*, n^*) = (1, 1)$ is stable only if $\delta_{11}^H < 0$. The potential interior equilibrium at x_+^* is always a saddle, and thus never stable. Whereas the equilibrium x_-^* can be either stable or unstable. The conditions for x_-^* to be unstable first require

$$\delta_{01}^H + \delta_{10}^L > 0 \tag{9}$$

and

$$\delta_{01}^H \delta_{10}^L > \delta_{11}^H \delta_{00}^L. \tag{10}$$

Instablity of x_-^* also requires

$$\epsilon < \epsilon_{\text{crit}}, \tag{11}$$

where ϵ is the speed of environmental feedback relative to speed of strategy updating. The value of ϵ_{crit} can be expressed analytically in terms of the parameters of the system, and differs for renewing and decaying resource feedbacks (See Supplementary information, sections S1.1 and S2.1).

Dynamical regimes Coupled strategy-environment dynamics exhibit several different qualitative dynamical regimes, depending on the incentives to switch strategies (δ's) and on the timescale separation, ϵ, between strategy evolution and environmental impacts.

When there is no incentive to lead the environmental movement or to lead the gold rush, as in Figure 2a, then both edge equilibria are stable, and only the saddle equilibrium falls within the state space. And so the dynamics in this regime will exhibit bistability – with attraction to one or the other edge equilibrium depending upon the initial conditions. Bistability is intuitive in this regime – because in neither high- nor low-quality environments is there any incentive for individuals to be leaders of change. And so the system will eventually be dominated by one or the other strategic type.

When there are positive incentives for individuals to lead the gold rush and to lead the environmental movement (Figure 2b), then neither edge equilibrium is stable. In this regime, because individuals are always incentivized to lead change, we might expect strategies and environmental quality to cycle. But positive incentives to lead change are not alone sufficient to induce cycles. Rather, cycles in this regime will occur only if the incentives to follow the environmental movement are also positive and stronger in aggregate than the incentive to lead these movements. Furthermore, cycles require that the environmental feedback is sufficiently slow compared to strategy evolution. In sum, when there are positive incentives to lead both movements, a stable limit cycle will occur when $\delta_{01}^H > 0$, $\delta_{10}^L > 0$, $\delta_{01}^H \delta_{10}^L > \delta_{11}^H \delta_{00}^L$, and the timescale condition 11 holds.

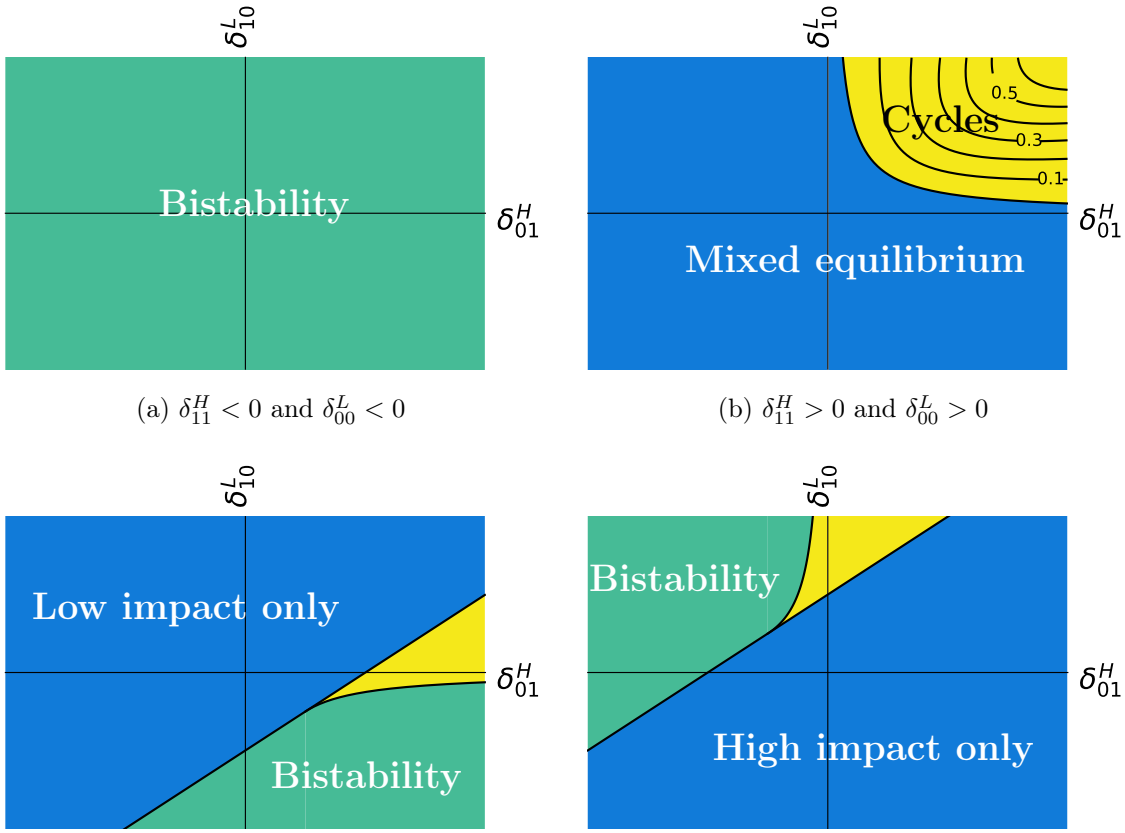
When there are positive incentives to lead the environmental movement but not to lead

the gold rush (Figure 2 c), then the low-impact dominated state will always be stable, and the high-impact state will always be unstable. In this regime we might expect only a single monomorphic equilibrium. However, a single edge equilibrium, bistability, and even stable limit cycles can all occur in this regime. In the blue-shaded region of figure 2 c there are no interior equilibria, so the system will settle on low-impact strategists alone. In the yellow and green regions, however, there are two interior equilibria, one of which is a saddle and one which can be stable or unstable. In the green region, one of the interior equilibria is a saddle the the other is stable, producing bistability between a low-impact monomorphic population and a mixed population. In the yellow region, however, limit cycles can occur provided the the environmental feedback is slow enough (condition 11), but not too slow. The yellow region can also produce bistability or a monomorphic population, depending upon the rate of environmental feedback (Figure 3).

When there are positive incentives for leaders of the gold rush but not the environmental movement (Figure 2 d), the high-impact dominated state will always be stable and the low-impact state unstable. Here again we might expect only a single monomorphic equilibrium – but, in fact, the dynamics also permit bistabilty and even limit cycles, depending upon the timescale of environmental feedbacks, analogous the the regime in figure 2 c.

This gives a complete picture of the possible outcomes that can arise in a two-strategy game described by a environmentally-dependent payoff matrix $\Pi(n)$ (for a detailed analysis, see supplementary information section S1.2). The most striking outcome pertains to when, and how, cyclic dynamics can arise in such eco-evolutionary games. While intuition would suggest cycles can arise when the incentives to lead and follow change are all positive, we have seen, to the contrary, that these conditions are neither necessary nor sufficient for cyclic dynamics. And whenever cycles do arise, they depend on a sufficient separation of timescales between strategy dynamics and environmental dynamics. Further, we find a complex array of different dynamical outcomes, including mixed equilibria, bistability, cycles, and dominance by one strategy.

Our analysis has assumed that payoffs are linear in the state of the environment and the frequencies of the strategies in the population. These assumptions allowed us to characterize all possible outcomes in terms of a few parameters. While these simplifying assumptions may seem to limit the range of applicability, in the remainder of the paper we highlight scientifically and societally relevant cases that fall within our model, as well as examples that extend beyond the framework analyzed here.



(a) $\delta_{11}^H < 0$ and $\delta_{00}^L < 0$

(b) $\delta_{11}^H > 0$ and $\delta_{00}^L > 0$

(c) $\delta_{11}^H < 0$ and $\delta_{00}^L > 0$

(d) $\delta_{11}^H > 0$ and $\delta_{00}^L < 0$

Figure 2: Dynamical outcomes of linear eco-evolutionary games. Each panel shows the dynamical outcomes for fixed values of incentives δ_{11}^H and δ_{00}^L. Yellow regions denote parameter regimes that can produce limit cycles, provided $\epsilon < \epsilon_{\text{crit}}$, with level curves of ϵ_{crit} shown as black lines. Blue regions represent regions with a single dynamical outcome. Green regions represent bistability. In panels (c) and (d) the yellow regions can exhibit bistability, dominance by one strategy, or cycles that occur in a bistable regime; the value of ϵ determines which of these outcomes occur. Supplementary Information section S1.2 provides analytical expressions for the boundaries between these dynamical regimes, in terms of the incentive parameters $\delta_{01}^H, \delta_{10}^L, \delta_{11}^H, dt_{00}^L$.

2.2 Importance of timescales

Our analysis above reveals qualitatively distinct dynamic regimes that depend on the incentives to switch strategies in a rich or poor environment. One regime (panel b in figure 2) features either an interior equilibrium or a limit cycle about that equilibrium. Payoff matrices in this regime that produce cyclic dynamics require that the net incentive to be a follower of change is stronger than the incentive to be a leader, and further that the relative time-scale of strategy evolution is fast relative to environmental impacts (low ϵ). This can lead to overshoot of the interior equilibrium, resulting in cycles. Figure 3 illustrates the importance of the relative timescales by showing two simulations that vary only in a single parameter value. Changing ϵ to make the relative speed of resource dynamics slower results in a stable limit cycle instead of a stable interior equilibrium.

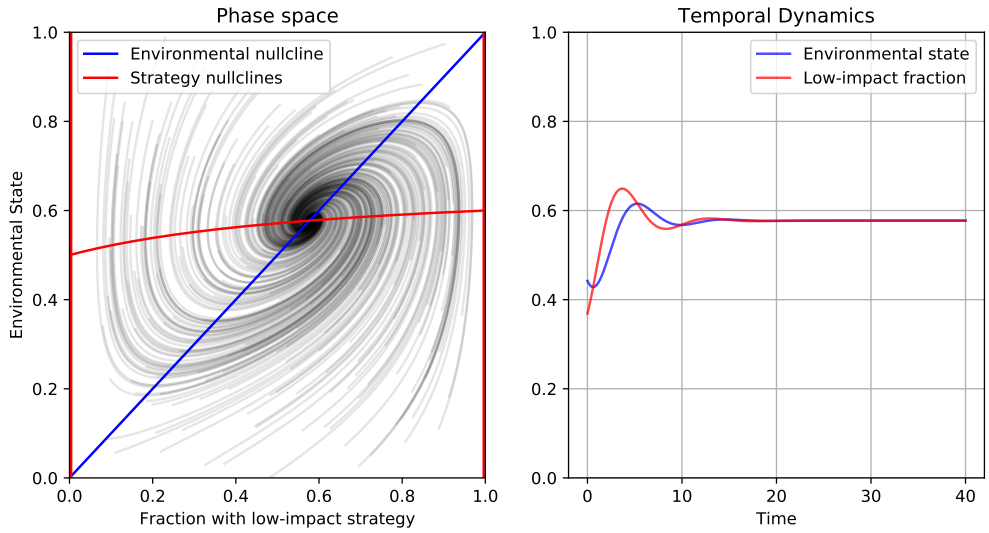
The speed of environmental feedbacks play an important role in determining both the stability characteristics of equilibria and the basins of attraction of equilibria. Figure 4 shows the approximate basins of attraction for two equilibria under environmental dynamics of different speeds. These figures correspond to the region of potential cycles in panel (c) of figure (2).

3 Case studies

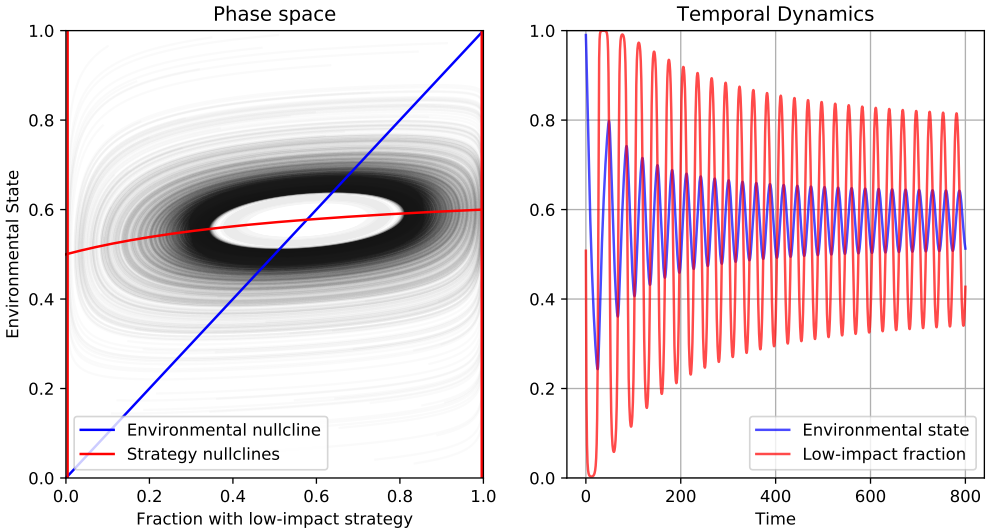
A large collection of prior studies on environment-strategy feedbacks, across a range of disciplines, can be be understood as instances of our general framework. The dynamical properties of these models are all predicted by our general analysis of such systems. We briefly review these models to highlight the broad applicability of our framework and to showcase the diversity of dynamical phenomena that occur in eco-evolutionary games.

3.1 Co-evolution of the environment and decision-making

Rand et al. (2017) developed a psychological model of decision-making where individuals can either make automatic "hardwired" decisions, or can make controlled decisions that are flexible and can shape a beneficial state of the environment. Although the motivation of their model is far from ecology, their model is in fact a special case of the decaying resource model. Rand et al. found that under certain circumstances these feedbacks can lead to cyclical dynamics: automatic and controlled agents cycle in abundance as the environment fluctuates in its favorability towards these the two cognitive styles. Rand et al. (2017) motivate their study by noting that controlled decision making is likely to be costly but will allow individuals to choose optimal behavior. Further, they assume that when a population is

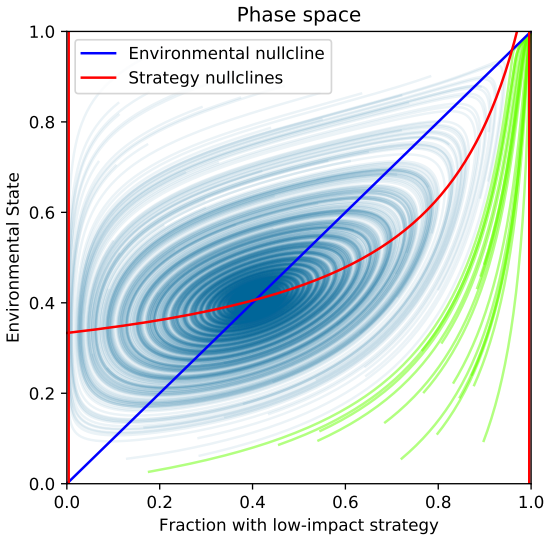


(a) Fast environmental dynamics, $\epsilon = .65$

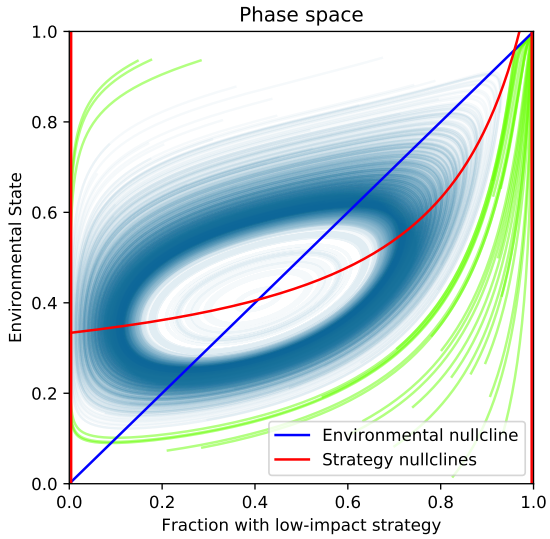


(b) Slow environmental dynamics, $\epsilon = 0.063$

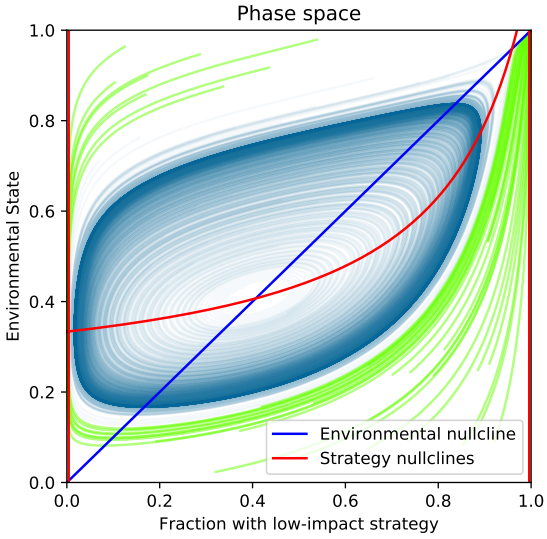
Figure 3: Phase planes and temporal dynamics in eco-evolutionary games with a decaying resource. Parameters are chose to fall in the yellow region of figure 2(b). Only the speed of environmental dynamics relative to strategy dynamics, ϵ, varies between the panels. Convergence either to an interior equilibrium or to a limit cycle is determined by ϵ. ($\alpha = 1, \delta_{11}^H = 2, \delta_{10}^H = 1, \delta_{01}^L = 3, \delta_{00}^L = 1$)



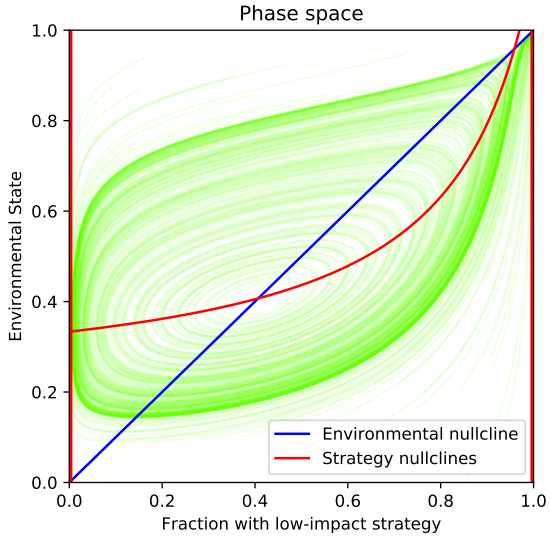
(a) Fast environmental dynamics, $\epsilon = .3$



(b) Intermediate environmental dynamics, $\epsilon = .261$



(c) Intermediate environmental dynamics, $\epsilon = .25$



(d) Slow environmental feedbacks, $\epsilon = .235$

Figure 4: Simulations of eco-evolutionary game dynamics from the regime with possible cycles in figure 2(c). In each panel, the color of the solution curves illustrate the basins of attraction of the system. Green curves approach the state dominated by the low impact strategy and blue curves represent regions that approach the interior equilibrium or a stable limit cycle. Panel (a) shows the dynamics with fast environmental feedbacks, and thus the interior equilibrium is stable, and has a large basin of attraction. Panels (b) and (c) illustrate cases with environmental dynamics of intermediate speed which exhibit bistability between the low-impact dominated state and limit cycles in the interior of the phase space. Panel (d) displays dynamics under slow environmental feedbacks. When feedback speed crosses a critical threshold, limit cycles are no longer possible, and the entire phase space approaches the corner equilibrium. ($\alpha = 1, \delta^H_{11} = -1/8, \delta^H_{10} = 1, \delta^L_{01} = 4, \delta^L_{00} = 2$)

dominated by controlled agents, then the fitness difference between optimal and suboptimal decisions will decrease because institutions or public goods created by controlled agents will stabilize the environment. This then favors automated agents who choose an option quickly without paying the cost of controlled processing. Rand et al. (2017) introduce a parameter that makes the cost of control frequency-dependent, so that when control agents are rare, it is more costly for them to ensure a stable environment.

The minimal model by Rand et al. is a special case of our decaying resource framework, as we prove in supplementary information section S3. By mapping their model onto our general framework the dynamical properties are immediately understood in terms of the incentive parameters of our general analysis. In particular, we find that the Rand et al. model falls within panel (b) of Figure 2 – i.e. there are positive incentives to lead change. Embedding their model as special case of linear eco-evolutionary games allows us to show, for example, that in the absence of a frequency-dependent cost of being a controlled agent, cycles are not possible, because the model then falls outside of the yellow region of Figure 2b. Further, we can use our framework to compute the critical time lag that produces cycles between cognitive styles, coupled with environmental cycles.

3.2 Grass-legume competition

Evo-evolutionary games provide a natural framework for studying competition between grasses and legumes. Many legumes form symbioses with nitrogen-fixing bacteria, allowing them to thrive in nitrogen-poor environments. Through time, however, some of the fixed nitrogen becomes available in the soil to nearby plants. In effect, the plant strategy of nitrogen fixation both frees plants from nitrogen limitation, and it generates an environmental feedback that increases the availability of nitrogen in the soil. Grasses, on the other hand, do not fix nitrogen. Competition between nitrogen fixing legumes and grasses can be modeled as a special case of our decaying resource framework. Here the environmental state corresponds to available nitrogen, and the two strategies correspond to the species present in the system. We can thus write the relative abundance of legumes as x and the relative abundance of grasses as $1 - x$.

We can determine what type of qualitative dynamics will arise in grass-legume competition, based on the four δ parameters and the relative timescale of environmental versus strategy dynamics. First, consider the grass-dominated state, with nitrogen availability at its lowest. In this state, we expect legumes to be able to invade because of the advantage of nitrogen fixation in a low-nitrogen environment. Thus we expect $\delta_{00}^{H} > 0$. Similarly, we expect $\delta_{11}^{L} > 0$ because in a high-nitrogen environment that is dominated by nitrogen

fixing legumes, non-fixing grasses will be able to invade since they do not pay the cost for fixing nitrogen, but can reap the benefit of a nutrient-rich environment. Thus, we know that the dynamics will fall somewhere in figure 2 b. Legumes are likely to have a competitive advantage in a low nitrogen environment regardless of their relative abundance, thus we expect $\delta_{01}^H > 0$. The same holds for grasses, given high nitrogen availability, so that $\delta_{10}^L > 0$. Finally, in species competition, it is typically more difficult for the first individual to successfully invade and establish than it is for an established species to spread and increase in abundance (Tilman, 2004). This implies that we expect $\delta_{00}^H < \delta_{01}^H$ and $\delta_{11}^L < \delta_{10}^L$.

Therefore $\delta_{00}^H \delta_{11}^L < \delta_{01}^H \delta_{10}^L$ will hold and so we expect grass-legume systems to be susceptible to cyclic dynamics. However, cyclic dynamics will still require that the timescale of the feedback between legumes and nitrogen availability is sufficiently slow. This too is reasonable because nitrogen is a valuable resource, so a legume has a strong incentive to limit the rate at which the nitrogen it fixes leaks into the environment.

A related kind of cycling dynamic can occur between available soil nitrogen and nitrogen-fixation strategies of the rhizobium bacteria. Theoretical (Akçay and Simms, 2011) and empirical (Weese et al., 2015) findings indicate that high nitrogen availability favors rhizobia that fix less nitrogen, while low nitrogen favors strains that fix more. This suggests that the necessary conditions for cycling can also occur in coupled nitrogen-strain frequency dynamics.

3.3 Common-pool resource harvesting

Our final case study is a classic example of linked strategy and environmental dynamics: common-pool resource harvesting. There is extensive literature on common-pool harvesting, which forms the basis for bioeconomics (Clark, 1990). Eco-evolutionary game theory provides a natural framework to situate common-pool resource models – because strategic interactions depend upon, and conversely influence, the abundance of the common-pool resource.

One might imagine that even the simplest form of common-pool resource harvesting may lead to cyclic dynamics: as the biomass of resource stock collapses and overshoots, harvesters respond by reducing effort, until the resource rebounds and high-effort strategies are again profitable. Surprisingly, our analysis shows that such cycles will never occur without additional complications. We formulate common-pool resource dynamics by assuming individuals can harvest with either high, e_H, or low, e_L, effort. We let the evolutionary process on strategy frequencies be governed by a profit function,

$$\pi(e_i, \eta) = pq\eta e_i - we_i, \tag{12}$$

that maps the resource level and harvest effort into fitness. As before, we assume that the

resource, η, is governed by logistic growth, and the harvest rate is proportional to η and effort. Since $\pi(e_i, \eta)$ is linear, this model is a special case of the general renewable resource model we have exhaustively analyzed.

Transforming the resource level into a normalized environmental metric (See Supplementary Information section (S4)), we can construct a payoff matrix, $\Pi(n)$ that maps the common-pool resource harvesting model onto general framework of eco-evolutionary games. The resulting values of incentives δ satisfy $\delta_{11}^H = \delta_{01}^H > 0$ and $\delta_{00}^L = \delta_{10}^L > 0$ when there are positive profits at the environmental state resulting from pure low-impact strategists and negative profits at the environment resulting from pure high-impact strategists. Under these profit assumptions, the common-pool resource system falls at the boundary of the blue and yellow regions of Figure 2b – i.e. incentives to lead and follow change are all positive, but the there is no (positive) value of ϵ that produces cycles. And so the only possible outcomes of this common-pool system is a stable mix of low- and high-impact strategists. However, since the system falls on the boundary of the cycling region, small changes to the system may be able to induce cyclic dynamics (see Supplementary Information section (S4) for other possible profit scenarios).

4 Non-linear eco-evolutionary games

So far, we analyzed eco-evolutionary games in which the payoffs to strategies are linear in both resource and strategy frequencies. In this section, we consider two phenomena that generate non-linear eco-evolutionary games and we study the dynamics they generate.

4.1 Common-pool resource harvesting with market pricing

In the simplest common-pool resource harvesting model the price received for each unit of harvested resource is constant. A fixed price makes sense when the system represents a small part of a large or global market, because local supply can have only a small impact on the global price. However, if the markets for the resource are local or the suppliers in consideration account for a significant portion of total supply, we expect the price of the harvested resource to be a function of the total harvest at the present time, resulting from the consumer demand function (Varian, 2010, Chapter 6). Here, we study how such market pricing alters the dynamics of coupled common pool resource-strategy dynamics. In particular, even though one might expect that market pricing could lead to overshooting of equilibria, we show that cycling still cannot occur in the common-pool resource system even with non-linearities introduced by market pricing.

A profit function with harvest-dependent prices can be written as

$$\pi(e_i, x, n) = p(h)qne_i - we_i \tag{13}$$

where $h = nq(xe_L + (1-x)e_H)$ and $p(h)$ is the market price as a function of resource supply. Notably, this model is not a special case of the framework presented in section 2.1 since there are higher order terms due to the dependency of the price of the resource on the state of the system. For simplicity we assume that the market price is linearly decreasing in the quantity supplied. Specifically, we set $p(h) = p_0(1 - \gamma h)$.

The non-linearity introduced by this profit function increases the range of dynamical outcomes (See supplementary information figure S2). Despite this, cyclic dynamics cannot occur. In supplementary information section S5.1 we conduct stability analyses of equilibria, showing that cycles cannot occur and that the stability of the equilibria does not depend on the degree of timescale separation, ϵ. This surprising result occurs because market pricing, though introducing non-linearity in the profit function, effects all harvesters in the same way, and thus does not provide the extra driver of cycles that strategic interactions can introduce.

4.2 Common-pool resource harvesting with efficiency gains

In this section we extend the common-pool resource model to account for a harvest efficiency, q, that depends on the frequency of a strategy. This model is again not a special case of the general renewable resource model outlined in section (2.1). The payoff function, however, is a special case of the payoff matrices considered in section (2.1). Differential harvesting efficiency may arise if, for example, low-effort harvesters share information about the state and location of the resource. This would lead to increasing harvest efficiency, q, with the fraction of the population who harvest with low effort, x. Alternatively, each strategy may require specialized skills and labor – and as a strategy increases in frequency, increased opportunities for social learning may lead to increased proficiency and efficiency gains (Henrich, 2004; Smolla and Akcay, 2018). Efficiency gains permit limit cycles in the common-pool resource system (Figure 5), depending on the relative speed of the resource versus strategy dynamics.

We formalize efficiency gains by introducing a catchability function, $q(x)$ that increases linearly in x for low-effort harvesters, and decreases in x for high-effort harvesters. For low effort harvesters we let $q_L(x) = q_0(1 + \alpha_L x)$ and for high effort harvesters we let $q_H(x) = q_0(1+\alpha_H(1-x))$ such that, all else being equal, harvest rates increase with increase prevalence of a strategy, and the magnitude of the benefit of increased frequency is controlled by α_L

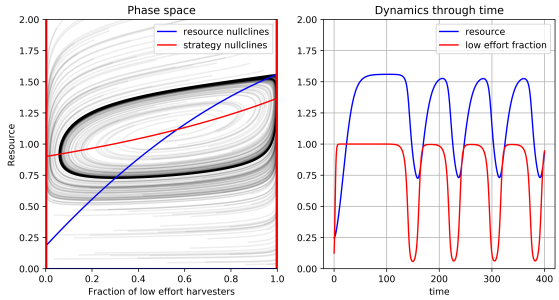


Figure 5: Phase plane and temporal dynamics of common-pool resource harvesting with frequency-dependent harvesting efficiency. The dynamics show convergence to a stable limit cycle. ($r = 0.33, K = 4, q = 0.5, e_L = 0.33, e_H = 0.6, p = 10, w = 5, \epsilon = 0.8, \alpha_L = 0.22, \alpha_H = 0.05$)

and α_H. The profit of each strategy can now be written as

$$\pi_L(x, n) = pq_0(1 + \alpha_L x)ne_L - we_L \tag{14a}$$

$$\pi_H(x, n) = pq_0(1 + \alpha_H(1 - x))ne_H - we_H \tag{14b}$$

When $\alpha_L = \alpha_H = 0$, this model reduces to the simple common-pool resource model. When either of these parameters are positive, however, the model falls outside the scope of linear eco-evolutionary games, but we can nonetheless analyze the dynamical outcomes (see Supplementary Information section S6).

Variable harvest efficiency alters both payoffs to individuals and the dynamics of the resource. As a result of these intertwined consequences, we find instances of non-monotonicity – where increasing the growth rate of the resource, for example, can first destabilize and then stabilize an interior equilibrium (see supplementary information Figure S3). While this variant of the common-pool resource model falls outside the scope of the general framework we have analyzed in detail, the intuition developed from our general framework still applies here. In particular, our analysis of linear eco-evolution games (Section 3.3) showed that increasing the values of either δ_{01}^H or δ_{10}^L were would permit cycles, by moving the system away from boundary of yellow and blue regions in Figure 2b. Frequency-dependent harvest efficiency plays a very similar role to increasing δ_{01}^H or δ_{10}^L – making it more profitable to switch to a high-frequency strategy due to increased efficiency – which help explains the cyclical dynamics that arise in this case.

Our model of a common-pool resource with variable harvesting efficiency is analogous to models of ostracism in common-pool systems (Tavoni et al., 2012). While the details differ, both models feature added costs associated with strategies that are at low frequency – and

the dynamical implications are qualitatively the same. As this analogy illustrates, there are many causes of frequency dependence in common-pool resource systems, and the framework we have developed allows the consequences to be understood generally.

5 Discussion

We have developed a framework for studying linked environmental and evolutionary game dynamics. Our analysis provides a systematic account of dynamical outcomes for an arbitrary game with linear payoff structures, for environments that either intrinsically grow or decay. This framework applies to any game-theoretic interaction where the strategies that individuals employ impact the environment through time, and the state of the environment influences the payoffs of the game. Such linkages are common in social-ecological systems, evolutionary ecology, and even psychology.

Despite the broad relevance of eco-evolutionary games, the role of the environment on strategic interactions has typically been considered only implicitly. Explicitly accounting for environmental feedbacks in these systems reveals added complexity and nuance (Estrela et al., 2018). We have shown that many prior studies of strategic interactions with environmental feedbacks are special cases of our general framework, with an explicit mapping to the parameters of our general framework.

Our framework reveals that the rich dynamical outcomes that arise in eco-evolutionary games can be understood in terms of four intuitive parameters (Figure 2). Each parameter represents the incentive for an individual to switch strategies when the environmental state is at one or the other extreme. Our analysis has highlighted dynamical outcomes that cannot occur without explicit consideration of environmental feedbacks. Perhaps the most striking result is that the timescale of environmental dynamics alters the basins of attraction of equilibria, and in some parameter regions cyclic dynamics can only occur under sufficiently slow environmental dynamics compared to strategy dynamics. This result extends that of Weitz et al. (2016), who found heteroclinic cycles independent of timescale separation in a special case of a resource with no intrinsic tendency to increase or decrease.

Coupling between strategic payoffs and the state of a renewing or decaying resource can induce cyclic dynamics even though neither the intrinsic environmental or intrinsic strategic dynamics exhibit cycles on their own. However, it is well known that many ecological systems can produce complex environmental dynamics even without feedback from individual actions (Turchin, 2003). Intrinsic complexity can result from multiple interacting environmental factors or a single environmental factor that is subject to age- or stage-structured population dynamics. In these cases, the complexity introduced via coupling with strategic

interactions is likely to be even more rich, with the potential for chaotic dynamics.

Structured interactions, arising from environmental heterogeneity, network structure, and spatial structure will add further complexity. Spatial models of environmental feedbacks indicate that feedbacks can lead to correlations between strategies and their environment, with consequences for the stability of cooperation (Pepper and Smuts, 2002; Hauert et al., 2018). Spatially structured interactions, and more generally, network structured interactions among individuals can fundamentally alter predictions about the strategies that will be successful in a system, but it is not well know what effects such structured interactions will have on a system where strategies and the environment are coupled. We suspect that it could lead to environmental heterogeneity and the simultaneous support of many strategies with differing environmental and strategic consequences.

We focused most of our analysis on linear two-strategy eco-evolutionary games. And yet non-linearities in the payoff structure of strategic interactions have important effects. We have seen that introducing non-linear payoffs, through market pricing, in a common-pool resource harvesting model generates a broader class of qualitative outcomes (see Supplementary Information Figure S2), and the possibilities under a general non-linear payoff functions are likely even broader. Further, as the size of the strategy space increases, so does the dimensionality of the dynamical system. If new strategies emerge then the game itself can evolve (Worden and Levin, 2007), leading to novel interactions with the environment. These extensions make it clear that eco-evolutionary games can be seen as complex adaptive systems with emergent properties that are not easily predicted from the environmental dynamics or the evolutionary game structure alone.

In human societies, the institutions structuring social interactions can be regarded as part of the environment, and co-evolve with strategic behaviors (Ostrom, 1990; Douglass, 1990; Bowles et al., 2003; Tilman et al., 2017). One can represent the institutional environment in our framework by constructing an institutional metric that modulates the game being played. More realistically, institutions will interact with an explicit resource and affect the incentives individuals face in a given environment, or how strategies affect environmental dynamics. For example, the success of international environmental agreements to achieve environmental stewardship depends on how individuals and nations respond to their incentives under a changing environment. In the context of pollution control and climate change mitigation, action is an intertemporal public good, with benefits of individual action accruing to a large population and in the future (Hauser et al., 2014). Policies of individual nations are likely to have feedbacks on the international institutional setting, the environment and the choices that individuals make. In these contexts, forecasting and discounting of the future will also play a central role (Arrow et al., 1996), and one that has received little attention in

evolutionary game theory.

Rather than being the exception, environmental feedbacks in strategic interactions are the norm. Explicitly accounting for such feedbacks reveals commonalities among many societally relevant systems, ranging from the psychology of decision-making to species interactions and climate-change action, and alters predictions about expected outcomes in such systems. Thus, incorporating strategy-environment feedbacks into evolutionary game theory is paramount.

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Supplementary Information

S1 Renewable resource model

We analyze a two-strategy evolutionary-game-theoretic model that incorporates environmental feedbacks, governed by renewable resource dynamics. Suppose that there is a resource stock, m, that in the absence of consumption or harvest pressure grows logistically, and is diminished through harvesting or consumption that is associated with the strategies in a game. For a 2-strategy game, let e_L and e_H be the resource harvest effort of strategies L and H, respectively, where we assume, that $e_L < e_H$. The dynamics of m are governed by

$$\frac{dm}{dt} = rm\left(1 - \frac{m}{k}\right) - qm\left(e_L x + e_H(1-x)\right) \tag{S1}$$

where x is the fraction of the population playing strategy L, r is the intrinsic rate of growth, k is the carrying capacity of m, and q is a parameter that maps resource degradation pressures (or harvesting efforts) (e_L, e_H) onto the rate of reduction in the resource. We assume that environmental impact rates are restricted so that m will be positive at equilibrium. This implies that $e_H \in [0, r/q)$ and $e_L \in [0, e_H)$.

Let $n \in [0,1]$ be a normalized measure of the state of the environment that maps onto the payoff structure of the game. We relate m to n with the linear relationship

$$n = \frac{m - k\left(1 - \frac{qe_H}{r}\right)}{(e_H - e_L)\frac{qk}{r}} \tag{S2}$$

so that when the whole population chooses strategy L, corresponding to harvesting pressure e_L, the equilibrium value of m maps to the environmental metric $n = 1$. Similarly, if the whole population adheres to strategy H, with e_H environmental pressure, $n \to 0$.

Next, suppose that the state of the environment influences the payoffs of the game. We use a payoff matrix for a 2-strategy game with payoffs that are dependent on the normalized environmental measure, n, given by

$$\Pi(n) = (1-n)\begin{bmatrix} R_0 & S_0 \\ T_0 & P_0 \end{bmatrix} + n\begin{bmatrix} R_1 & S_1 \\ T_1 & P_1 \end{bmatrix} \tag{S3}$$

so that the matrix entries correspond to the payoffs of the game under conditions of a low or high environmental state. We can write the payoff for playing strategy L and strategy H

as

$$\pi_L(x,n) = (1-n)(R_0 x + S_0(1-x)) + n(R_1 x + S_1(1-x)) \tag{S4a}$$

$$\pi_H(x,n) = (1-n)(T_0 x + P_0(1-x)) + n(T_1 x + P_1(1-x)). \tag{S4b}$$

Following the replicator equation, the payoffs from the game determine the evolution of the proportion of the population that plays each strategy. In all, we can write our system as

$$\epsilon \dot{x} = x(1-x)(\pi_L(x,n) - \pi_H(x,n)) \tag{S5a}$$

$$\dot{n} = (r - q(e_L n + e_H(1-n)))\,(x-n). \tag{S5b}$$

We let $\tau = t/\epsilon$ and re-scale time so that our system can be written as

$$x' = x(1-x)(\pi_L(x,n) - \pi_H(x,n)) \tag{S6a}$$

$$n' = \epsilon\,(r - q(e_L n + e_H(1-n)))\,(x-n). \tag{S6b}$$

where $\frac{dx}{d\tau} = x'$.

S1.1 Renewable resource stability analysis

This model has up to four equilibria within the state space. We have 2 edge equilibria, at $(x^*, n^*) \in \{(0,0),(1,1)\}$ and up to two interior equilibria that occur when $\pi_L(x,n) = \pi_H(x,n)$ and $n = x$. While there are up to two points that meet the criterion for a potential interior equilibrium, they need not fall inside the state space. Also, note that while $n' = 0$ at $n = \frac{e_H - r/q}{e_H - e_L}$ this too falls outside of our state space since we assume that $e_H \in (0, r/q)$ and $e_L \in (0, e_H)$.

At the edge equilibria, stability conditions are simple. At $(x^*, n^*) = (0,0)$, stability occurs if and only if $P_0 > S_0$. At At $(x^*, n^*) = (1,1)$, stability occurs if and only if $R_1 > T_1$.

Next, we analyze the conditions for stability of interior equilibria. The interior equilibrium, defined by $\pi_L(x,n) = \pi_H(x,n)$ occurs when

$$n = \frac{(S_0 - P_0)(1-x) + (R_0 - T_0)x}{(P_1 - S_1 + S_0 - P_0)(1-x) + (T_1 - R_1 + R_0 - T_0)x} \tag{S7}$$

and substituting $x = n$ will yield the positions of interior equilibria. We can substitute and solve for the equilibrium level of the environmental indicator and the equilibrium strategy

fraction, which is

$$n^*_\pm = x^*_\pm = \frac{2(S_0 - P_0) - R_0 + T_0 - S_1 + P_1 \pm \sqrt{(P_1 - S_1 + T_0 - R_0)^2 + 4(S_0 - P_0)(T_1 - R_1)}}{2(S_0 - P_0 + P_1 - S_1 - R_0 + T_0 - T_1 + R_1)}. \tag{S8}$$

The analysis can be streamlined defining four values as

$$\begin{aligned}
\delta^H_{11} &= \pi_H(1,1) - \pi_L(1,1) = T_1 - R_1 \\
\delta^H_{01} &= \pi_H(0,1) - \pi_L(0,1) = P_1 - S_1 \\
\delta^L_{10} &= \pi_L(1,0) - \pi_H(1,0) = R_0 - T_0 \\
\delta^L_{00} &= \pi_L(0,0) - \pi_H(0,0) = S_0 - P_0.
\end{aligned} \tag{S9}$$

Using these δ's allows us to write the interior equilibrium location as

$$x^*_\pm = n^*_\pm = \frac{2\delta^L_{00} + \delta^H_{01} - \delta^L_{10} \pm \sqrt{(\delta^H_{01} - \delta^L_{10})^2 + 4\delta^H_{11}\delta^L_{00}}}{2(\delta^L_{00} + \delta^H_{01} - \delta^L_{10} - \delta^H_{11})}. \tag{S10}$$

Stability at such an equilibrium can be computed from the Jacobian matrix evaluated at an interior equilibrium, which is

$$J^* = \begin{bmatrix} x(1-x)\frac{\partial g}{\partial x}(x,n) & x(1-x)\frac{\partial g}{\partial n}(x,n) \\ \epsilon\left(r - q(e_L n + e_H(1-n))\right) & -\epsilon\left(r - q(e_L n + e_H(1-n))\right) \end{bmatrix}_{(x,n)=(x^*,n^*)} \tag{S11}$$

where $g(x,n) = \pi_L(x,n) - \pi_H(x,n)$. Stability requires $\mathrm{Det}(J^*) > 0$ and $\mathrm{Tr}(J^*) < 0$.

First, consider the determinant of the Jacobian matrix,

$$\mathrm{Det}(J^*) = -\epsilon\left(r - q(e_L n^* + e_H(1-n^*))\right) x^*(1-x^*)\left(\frac{\partial g}{\partial n}(x^*,n^*) + \frac{\partial g}{\partial x}(x^*,n^*)\right). \tag{S12}$$

Due to the restrictions on the level of environmental impact, $e_H \in (0, r/q)$ and $e_L \in [0, e_H)$, and the fact that both x and n are between zero and one, we can conclude that $\mathrm{Det}(J^*) > 0$ if and only if $\frac{\partial g}{\partial n}(x^*,n^*) + \frac{\partial g}{\partial x}(x^*,n^*) < 0$. The terms of interest are

$$\frac{\partial g}{\partial n}(x^*,n^*) = -\left[(\delta^H_{01} + \delta^L_{00})(1-x^*) + (\delta^L_{10} + \delta^H_{11})x^*\right] \tag{S13a}$$

$$\frac{\partial g}{\partial x}(x^*,n^*) = (\delta^L_{10} - \delta^L_{00})(1-n^*) + (\delta^H_{01} - \delta^H_{11})n^* \tag{S13b}$$

Recalling the at an interior equilibrium $x^* = n^*$ we can simplify the expression for a positive

determinant of the Jacobian matrix to

$$\delta_{10}^{L} - \delta_{01}^{H} - 2\delta_{00}^{L} + 2(\delta_{01}^{H} - \delta_{10}^{L} - \delta_{11}^{H} + \delta_{00}^{L})x^{*} < 0 \tag{S14}$$

Evaluation at the equilibria yields the condition for a positive determinant, and is

$$\pm\sqrt{(\delta_{01}^{H} - \delta_{10}^{L})^{2} + 4\delta_{11}^{H}\delta_{00}^{L}} < 0. \tag{S15}$$

Where $\sqrt{(\delta_{01}^{H} - \delta_{10}^{L})^{2} + 4\delta_{11}^{H}\delta_{00}^{L}} < 0$ corresponds to x_{+}^{*} and $-\sqrt{(\delta_{01}^{H} - \delta_{10}^{L})^{2} + 4\delta_{11}^{H}\delta_{00}^{L}} < 0$ corresponds to x_{-}^{*}.

The trace of the Jacobian matrix is

$$\mathrm{Tr}(J^{*}) = x^{*}(1 - x^{*})\frac{\partial g}{\partial x}(x^{*}, n^{*}) - \epsilon\left(r - q(e_{L}n^{*} + e_{H}(1 - n^{*}))\right) \tag{S16}$$

where $g(x, n) = \pi_{L}(x, n) - \pi_{H}(x, n)$. Given $\mathrm{Det}(J^{*}) > 0$, stability at an interior equilibrium will occur if and only if $\mathrm{Tr}(J^{*}) < 0$. A sufficient condition for a negative trace is $\frac{\partial g}{\partial x}(x^{*}, n^{*}) < 0$, because this implies that both terms of the trace are negative. This occurs when either

$$\delta_{01}^{H} + \delta_{10}^{L} < 0 \tag{S17}$$

or

$$\delta_{10}^{L}\delta_{01}^{H} < \delta_{11}^{H}\delta_{00}^{L}. \tag{S18}$$

On the other hand if conditions S17 and S18 are violated, stability is still possible but not assured. In this scenario, stability depends on the relative speed of environmental feedbacks.

In this case, stability occurs at the interior equilibrium when

$$\epsilon > \epsilon_{\text{crit}} = \frac{\begin{aligned}&\left(\sqrt{4\delta_{11}^H\delta_{00}^L + (\delta_{01}^H - \delta_{10}^L)^2} - \delta_{01}^H - \delta_{10}^L\right)\\ &\times\left(\sqrt{4\delta_{11}^H\delta_{00}^L + (\delta_{01}^H - \delta_{10}^L)^2} - 2\delta_{11}^H + \delta_{01}^H - \delta_{10}^L\right)\\ &\times\left(\sqrt{4\delta_{11}^H\delta_{00}^L + (\delta_{01}^H - \delta_{10}^L)^2} - \delta_{01}^H + \delta_{10}^L - 2\delta_{00}^L\right)\end{aligned}}{\begin{aligned}&4(\delta_{11}^H - \delta_{01}^H + \delta_{10}^L - \delta_{00}^L)\\ &\times\Big[q((\delta_{01}^H - \delta_{10}^L)(e_H + e_L) - 2(\delta_{11}^H e_H - \delta_{00}^L e_L))\\ &+ q(e_H - e_L)\sqrt{4\delta_{11}^H\delta_{00}^L + (\delta_{01}^H - \delta_{10}^L)^2}\\ &+ 2r(\delta_{11}^H - \delta_{01}^H + \delta_{10}^L - \delta_{00}^L)\Big]\end{aligned}} \tag{S19}$$

where ϵ is the speed of environmental feedbacks relative to strategy updating. As r increases, the region of the parameter space that leads to a stable interior equilibrium increases. This makes sense, both ϵ and r increase the speed of environmental dynamics, and thus changes in these parameters have similar effects on outcomes.

S1.2 Renewable resource system-level analysis

The x_+^* equilibrium is an element of the unit interval when the following conditions hold:

$$x_+^* \in (0,1) \iff \begin{cases} [\delta_{00}^L + \delta_{01}^H - \delta_{10}^L - \delta_{11}^H > 0 \text{ and} \\ (\delta_{00}^L < 0 \text{ or } \delta_{01}^H - \delta_{10}^L + 2\delta_{00}^L > 0) \text{ and} \\ (\delta_{11}^H < 0 \text{ and } \delta_{01}^H - \delta_{10}^L - 2\delta_{11}^H > 0)] \\ \text{or} \\ [\delta_{00}^L + \delta_{01}^H - \delta_{10}^L - \delta_{11}^H < 0 \text{ and} \\ (\delta_{00}^L < 0 \text{ and } \delta_{01}^H - \delta_{10}^L + 2\delta_{00}^L < 0) \text{ and} \\ (\delta_{11}^H < 0 \text{ or } \delta_{01}^H - \delta_{10}^L - 2\delta_{11}^H < 0)] \end{cases} \tag{S20}$$

Similarly, the x^*_- equilibrium is an element of the unit interval when the following conditions hold:

$$x^*_- \in (0,1) \iff \begin{cases} [\delta^L_{00} + \delta^H_{01} - \delta^L_{10} - \delta^H_{11} > 0 \text{ and} \\ (\delta^L_{00} > 0 \text{ and } \delta^H_{01} - \delta^L_{10} + 2\delta^L_{00} > 0) \text{ and} \\ (\delta^H_{11} > 0 \text{ or } \delta^H_{01} - \delta^L_{10} - 2\delta^H_{11} > 0)] \\ \text{or} \\ [\delta^L_{00} + \delta^H_{01} - \delta^L_{10} - \delta^H_{11} < 0 \text{ and} \\ (\delta^L_{00} > 0 \text{ or } \delta^H_{01} - \delta^L_{10} + 2\delta^L_{00} < 0) \text{ and} \\ (\delta^H_{11} > 0 \text{ and } \delta^H_{01} - \delta^L_{10} - 2\delta^H_{11} < 0)] \end{cases} \tag{S21}$$

Ascertaining what these criteria mean for system-level properties of interest is simplified by considering four cases that span the values of δ^H_{11} and δ^L_{00}.

Case 1: ($\delta^H_{11} < 0$ and $\delta^L_{00} < 0$) In this case, both edge equilibria are stable and only an interior saddle equilibrium, given by x^*_+ falls in the interior of the state space. Thus, this corresponds to bistability of strategy L and H where the resulting environmental and strategy state depends on the initial environmental and strategy conditions. This result is invariant to the details of the environmental feedback timescale or the payoff structure of the game (other than the restriction that $\delta^H_{11} < 0$ and $\delta^L_{00} < 0$).

Case 2: ($\delta^H_{11} > 0$ and $\delta^L_{00} > 0$) In this case both edge equilibria are unstable, and only the x^*_- equilibrium is in the state space. The stability analysis indicates that x^*_- is guaranteed to be a stable equilibrium when either $\delta^H_{01} + \delta^L_{10} < 0$ or $\delta^H_{01}\delta^L_{10} < \delta^H_{11}\delta^L_{00}$. If both of these conditions are violated, then stability will governed by the condition on ϵ. When the interior equilibrium is stable, all initial conditions will lead to the interior equilibrium. When it is unstable, limit cycles will result from all starting conditions. These are the cases that correspond to the 'oscillating tragedy of the commons' in Weitz et al. (2016).

Case 3: ($\delta^H_{11} < 0$ and $\delta^L_{00} > 0$) In this case, both interior equilibria can fall within the state space, given all the following hold:

$$\begin{cases} |\delta^H_{01} - \delta^L_{10}| > 2\sqrt{-\delta^H_{11}\delta^L_{00}} \\ \delta^H_{01} - \delta^L_{10} > \delta^H_{11} - \delta^L_{00} \\ \delta^H_{01} - \delta^L_{10} > -2\delta^L_{00} \\ \delta^H_{01} - \delta^L_{10} > 2\delta^H_{11} \end{cases} \tag{S22}$$

For these four conditions to hold, given $\delta^H_{11} < 0$ and $\delta^L_{00} > 0$, we need either $\delta^H_{01} - \delta^L_{10} > 2\sqrt{-\delta^H_{11}\delta^L_{00}}$, or $\delta^H_{01} - \delta^L_{10} < -2\sqrt{-\delta^H_{11}\delta^L_{00}}$. The latter cannot hold simultaneously with the three

other conditions, since $-2\sqrt{-\delta_{11}^H\delta_{00}^L}$ must be less that at least one of the other terms that set minimums on $\delta_{01}^H - \delta_{10}^L$. Further, the right-hand-side of the first inequality is positive, while the rest are negative. Thus all four of the conditions hold if and only if $\delta_{01}^H - \delta_{10}^L > 2\sqrt{-\delta_{11}^H\delta_{00}^L}$. Also, since violating the first condition implies that interior equilibria cannot exist, there will either be two or zero interior equilibria (with a special case where the nullclines are tangent at one point). When there is no interior equilibrium, dynamics will tend toward the state where all individuals employ the strategy with low environmental impact. This state is stable, since $\delta_{11}^H < 0$. When there are two interior equilibria, one will be a saddle, and one will be stable or unstable depending on parameters and the degree of timescale separation. If this interior equilibrium is stable, then the resulting dynamics of the system will be similar to the bi-stable regime described above. If this interior equilibrium is unstable, the system may have limit cycles from some initial conditions and tend toward dominance of the low impact strategy from other initial conditions. It is also possible, for low values of ϵ, that a limit cycle will not exist, and instead dynamics will tent toward the low impact state from all initial conditions.

Case 4: ($\delta_{11}^H > 0$ and $\delta_{00}^L < 0$) Lastly, following similar arguments as in case 3, we conclude that two interior equilibria will result when $\delta_{01}^H - \delta_{10}^L < -2\sqrt{-\delta_{11}^H\delta_{00}^L}$, and no interior equilibria will occur if $\delta_{01}^H - \delta_{10}^L > -2\sqrt{-\delta_{11}^H\delta_{00}^L}$. In this case, the edge equilibrium where the high impact strategy dominates will always be stable. If there are two interior equilibria, then as in case 3, depending on the value of ϵ, either bi-stability, limit cycles embedded in a bi-stable regime, or dominance of the high impact strategy from all initial conditions will result.

S2 Decaying resource model

While some resources are intrinsically self-renewing, many others are intrinsically decaying, and are maintained by production as a consequence of agents' strategies. Here, we treat this case.

Let m be the concentration a resource that impacts the payoffs of players in a game, and is created as a byproduct playing the game. We assume that in the absence of production by players of the game, the concentration of m decays exponentially. We also assume that strategy L has a low emissions rate of the resource, e_L, and strategy H has a higher emissions rate rate, e_H. Given these assumptions we can model the dynamics of m as

$$\frac{dm}{dt} = -\alpha m + e_L x + e_H(1-x) \tag{S23}$$

where x is the fraction of the population that employs strategy L, and $(1-x)$ is the fraction of strategy H players. While m can be any resource that meets the assumptions above, a clear example with societal relevance is pollution. Many actions generate pollution, and stocks of pollution impact many systems. However, there is a more broad class of problems that also fit within this framework, including the cognition-environment feedbacks studied by Rand et al. (2017).

As in the case of the regenerating resource studied in the previous section, we define a metric of the environmental state, n,

$$n = \frac{e_H - \alpha m}{e_H - e_L} \tag{S24}$$

such that when the whole population has high emissions, e_H, $n \to 0$ and when the whole population has low emissions, e_L, $n \to 1$. Whereas m is a direct measure of the concentration of a resource stock, for example a pollutant, n is a normalized transformation of m that is used to write the payoff structure of the game being considered. Employing a change of variables, the dynamics of n can be modeled as

$$\dot{n} = \alpha(x - n). \tag{S25}$$

We use the same payoff matrix as before for the 2-strategy game with payoffs that are dependent on the normalized environmental measure, n, given by

$$\Pi(n) = (1-n)\begin{bmatrix} R_0 & S_0 \\ T_0 & P_0 \end{bmatrix} + n\begin{bmatrix} R_1 & S_1 \\ T_1 & P_1 \end{bmatrix} \tag{S26}$$

so that the matrix entries correspond to the payoffs of the game under conditions of a low or high environmental state. We can write the payoff for playing strategy L and strategy H as

$$\pi_L(x,n) = (1-n)(R_0 x + S_0(1-x)) + n(R_1 x + S_1(1-x)) \tag{S27a}$$

$$\pi_H(x,n) = (1-n)(T_0 x + P_0(1-x)) + n(T_1 x + P_1(1-x)) \tag{S27b}$$

when x is the fraction of the population that plays strategy L and has low emissions. Following the replicator equation, the payoffs from the game determine the evolution of the

proportion of the population that plays each strategy. In all, we can write our system as

$$\epsilon\dot{x} = x(1-x)(\pi_L(x,n) - \pi_H(x,n)) \tag{S28a}$$

$$\dot{n} = \alpha(x-n). \tag{S28b}$$

Let $\tau = t/\epsilon$ to re-scale time so that our system can be written as

$$x' = x(1-x)(\pi_L(x,n) - \pi_H(x,n)) \tag{S29a}$$

$$n' = \epsilon\alpha(x-n) \tag{S29b}$$

where $\frac{dx}{d\tau} = x'$.

S2.1 Decaying resource stability analysis

This model also has up to four equilibria within the state space. We have 2 edge equilibria, at $(x^*, n^*) \in \{(0,0),(1,1)\}$ and up to two interior equilibria that occur when $\pi_L(x,n) = \pi_H(x,n)$ and $n = x$.

We analyze the Jacobian matrix to derive the conditions for stability of interior equilibria. The Jacobian matrix for this system at an interior equilibrium is

$$J^* = \begin{bmatrix} x(1-x)\frac{\partial g}{\partial x}(x,n) & x(1-x)\frac{\partial g}{\partial n}(x,n) \\ \epsilon\alpha & -\epsilon\alpha \end{bmatrix}_{(x,n)=(x^*,n^*)} \tag{S30}$$

where, once again, $g(x,n) = \pi_L(x,n) - \pi_H(x,n)$. Also, the location of the interior equilibrium is the same as in the renewable resource model, with

$$n^* = x^* = \frac{2(S_0 - P_0) - R_0 + T_0 - S_1 + P_1 \pm \sqrt{(P_1 - S_1 + T_0 - R_0)^2 + 4(S_0 - P_0)(T_1 - R_1)}}{2(S_0 - P_0 + P_1 - S_1 - R_0 + T_0 - T_1 + R_1)}. \tag{S31}$$

Again, we use

$$\delta_{11}^H = T_1 - R_1 \tag{S32a}$$

$$\delta_{01}^H = P_1 - S_1 \tag{S32b}$$

$$\delta_{10}^L = R_0 - T_0 \tag{S32c}$$

$$\delta_{00}^L = S_0 - P_0 \tag{S32d}$$

to simplify our expressions and take into account only the differences in the payoffs, without

loss of generality. The simplified expression for the interior equilibrium is

$$n^* = x^* = \frac{2\delta_{00}^L + \delta_{01}^H - \delta_{10}^L \pm \sqrt{(\delta_{01}^H - \delta_{10}^L)^2 + 4\delta_{11}^H\delta_{00}^L}}{2(\delta_{00}^L + \delta_{01}^H - \delta_{10}^L - \delta_{11}^H)}. \tag{S33}$$

In relation to the analyses for the renewable resource model, the structure of the Jacobian matrix for the decaying resource model is very similar. This will make our analysis easier because much of it carries over directly from previous sections.

Stability at an interior equilibrium can be determined by trace and determinant of the Jacobian matrix. As before, the determinant is positive if and only if

$$\frac{\partial g}{\partial n}(x^*, n^*) + \frac{\partial g}{\partial x}(x^*, n^*) < 0 \tag{S34}$$

and a sufficient condition for a negative trace is

$$\frac{\partial g}{\partial n}(x^*, n^*) < 0. \tag{S35}$$

However, if condition S35 is violated but condition S34 holds, stability is still possible, and will depend on the speed of environmental feedbacks. In this case, the condition for stability is

$$\epsilon\alpha > \epsilon_{\text{crit}}\alpha = \frac{\begin{array}{c}\left(\sqrt{4\delta_{11}^H\delta_{00}^L + (\delta_{01}^H - \delta_{10}^L)^2} - \delta_{01}^H - \delta_{10}^L\right) \\ \left(\sqrt{4\delta_{11}^H\delta_{00}^L + (\delta_{01}^H - \delta_{10}^L)^2} - 2\delta_{11}^H + \delta_{01}^H - \delta_{10}^L\right) \\ \left(\sqrt{4\delta_{11}^H\delta_{00}^L + (\delta_{01}^H - \delta_{10}^L)^2} - \delta_{01}^H + \delta_{10}^L - 2\delta_{00}^L\right)\end{array}}{8(\delta_{11}^H - \delta_{01}^H + \delta_{10}^L - \delta_{00}^L)^2} \tag{S36}$$

so that fast enough environmental dynamics can stabilize any interior equilibrium, even if condition S35 is not met. Lastly, $g(x, n)$ is unchanged from the renewable resource model, implying that the forms of condition S35 and condition S34 also remain unchanged from the renewable resource model.

Now, we consider the edge equilibria. As before, at $(x^*, n^*) = (0, 0)$ stability occurs if and only if $\delta_{00}^L = S_0 - P_0 < 0$. Again, $(x^*, n^*) = (1, 1)$ is stable if and only if $\delta_{11}^H = T_1 - R_1 < 0$. Thus if both δ_{11}^H and δ_{00}^L are positive, then both edge equilibria are unstable.

S2.2 Decaying resource system-level analysis

For the decaying resource model, the system-level analyses do not change from the renewable resource model, and thus the regions of the parameter space as divided in figure 2 do not

change, and retain the same qualitative interpretations. This is because the position of the equilibria are unchanged and the sufficient conditions for stability of an interior equilibrium depend only on the δ parameters which share definitions in both systems. Thus, we can conclude that the only change to the system-level analysis from the renewable resource model is the value of ϵ_{crit} that divides cycles from a stable interior equilibrium in the regions of the parameter space where cycles can occur.

S3 Cognitive strategy dynamics as an eco-evolutionary game with decaying resource

Rand et al. (2017) present minimal model of automatic versus controlled processing with a cognition-environment feedback. In their model, the presence of controlled agents leads to an environment that favors automatic processing, and controlled processing is costly. They show that when the cost of control increases when there are fewer control agents, then cycles can result in what they term an "evolutionary pendulum". The minimal model presented in their paper is a special case of our decaying resource framework of game-environment feedbacks. In this section, we make the connection explicit.

First, we introduce the model from Rand et al. (2017). Let x be the fraction of controlled processing agents in the population. Then the fitness of each agent is

$$f_c = 1 - c - w(1 - x) \tag{S37a}$$

$$f_a = 1 - p \tag{S37b}$$

where c is the fixed cost of controlled processing, w is the extra cost of being a controlled processing agent when rare, and p is the environmentally dependent cost of automatic processing. This cost is governed by a “cognition-environment” feedback given by

$$\dot{p} = \frac{1}{\tau_p}\left((1 - x) - p\right) \tag{S38}$$

where τ_p governs the relative speed of this feedback. The dynamics of the frequency of the agents is governed by the replicator equation:

$$\dot{x} = x(1 - x)(f_c - f_a) \tag{S39}$$

This leads a complete system of equations given by

$$\dot{x} = x(1-x)(p - c - w(1-x)) \tag{S40a}$$

$$\dot{p} = \frac{1}{\tau_p}\left((1-x) - p\right). \tag{S40b}$$

Recall that the general decaying-resource model presented herein is given by

$$\dot{y} = y(1-y)(\pi_L(y,n) - \pi_H(y,n)) \tag{S41a}$$

$$\dot{n} = \epsilon\alpha(y-n) \tag{S41b}$$

where y is the fraction of the population with strategy L, n is a measure of the resource stock and $\pi_L(y,n)$ and $\pi_H(y,n)$ are the environmentally dependent payoffs from the game matrix

$$\Pi(n) = (1-n)\begin{bmatrix} R_0 & S_0 \\ T_0 & P_0 \end{bmatrix} + n\begin{bmatrix} R_1 & S_1 \\ T_1 & P_1. \end{bmatrix} \tag{S42}$$

If we transform the equations from Rand et al. (2017) by

$$n = p \tag{S43a}$$

$$y = 1 - x \tag{S43b}$$

we can write the dynamics of the new system as

$$\dot{y} = -\dot{x}(x = 1-y, p = n) \tag{S44a}$$

$$\dot{n} = \dot{p}(x = 1-y, p = n) \tag{S44b}$$

which simplifies to

$$\dot{y} = y(1-y)(wy + c - n) \tag{S45a}$$

$$\dot{n} = \frac{1}{\tau_p}(y-n). \tag{S45b}$$

Thus, if we let $\epsilon\alpha = 1/\tau_p$, $R_0 = 1$, $S_0 = 1$, $T_0 = 1 - c - w$, $P_0 = 1 - c$, $R_1 = 0$, $S_1 = 0$, $T_1 = 1-c-w$, and $P_1 = 1-c$ we can see that our general model from system of equations S41 becomes the same as a linear transformation of the Rand et al. (2017) minimal model. Thus the Rand et al. (2017) model is a special case of the decaying-resource model presented and analyzed in this paper. Given this, we could typically compute the δ's and from this know the location, stability and dynamics near the equilibria of the system. However, this model

is a 'special' special case, thus more analysis is needed to go from the general model to the results of Rand et al. (2017).

The δ values that govern the analysis are

$$\delta_{11}^H = T_1 - R_1 = 1 - c - w \tag{S46a}$$
$$\delta_{01}^H = P_1 - S_1 = 1 - c \tag{S46b}$$
$$\delta_{10}^L = R_0 - T_0 = c + w \tag{S46c}$$
$$\delta_{00}^L = S_0 - P_0 = c \tag{S46d}$$

these values for the δ's fall within the special case where

$$\delta_{11}^H - \delta_{01}^H + \delta_{10}^L - \delta_{00}^L = 0. \tag{S47}$$

This is a special case that we have yet to analyze for the general model, because it accounts for a small region of the parameter space. We proceed to analyze the general model given we are in this special case. We are interested in the stability of the interior equilibrium because this is the equilibrium point around which the cyclic dynamics occur in the Rand et al. (2017) model.

S3.1 Analysis

Assuming that $\delta_{11}^H - \delta_{01}^H + \delta_{10}^L - \delta_{00}^L = 0$ we analyze the general model with a decaying resource, given by

$$\dot{y} = y(1-y)g(y,n) \tag{S48a}$$
$$\dot{n} = \epsilon\alpha(y-n) \tag{S48b}$$

where y is the fraction of the population with strategy L, n is a measure of the resource stock and

$$g(y,n) = \pi_L(y,n) - \pi_H(y,n) = (1-n)(\delta_{10}^L y + \delta_{00}^L(1-y)) - n(\delta_{11}^H y + \delta_{01}^H(1-y)) \tag{S49}$$

is the gradient of selection. The interior equilibrium occurs where $g(y,n) = 0$ and $y = n$. The first condition holds when

$$n = \frac{\delta_{00}^L(1-y) + \delta_{10}^L y}{(\delta_{01}^H + \delta_{00}^L)(1-y) + (\delta_{11}^H + \delta_{10}^L)y}. \tag{S50}$$

In this special case, the denominator is equal to $A = \delta_{00}^L + \delta_{01}^H = \delta_{10}^L + \delta_{11}^H$. This simplifies our analysis and we can write the location of the interior equilibrium as

$$n = 1/A \left[\delta_{00}^L(1-y) + \delta_{10}^L y\right] \tag{S51}$$

which, implies that

$$n^* = y^* = \frac{\delta_{00}^L}{\delta_{11}^H + \delta_{00}^L}. \tag{S52}$$

Stability at this interior equilibrium can be derived from the Jacobian matrix evaluated at this equilibrium,

$$J^* = \begin{bmatrix} y(1-y)\frac{\partial g}{\partial y}(y,n) & y(1-y)\frac{\partial g}{\partial n}(y,n) \\ \epsilon\alpha & -\epsilon\alpha \end{bmatrix}_{(y,n)=(y^*,n^*)} \tag{S53}$$

where

$$\frac{\partial g}{\partial y}(y^*, n^*) = \frac{\delta_{11}^H(\delta_{10}^L - \delta_{00}^L) + \delta_{00}^L(\delta_{01}^H - \delta_{11}^H)}{\delta_{00}^L + \delta_{11}^H}$$

and

$$\frac{\partial g}{\partial n}(y^*, n^*) = -\delta_{00}^L - \delta_{01}^H = -A.$$

An unstable interior equilibrium will occur when $\mathrm{Det}(J^*) > 0$ and $\mathrm{Tr}(J^*) > 0$, and this will lead to cycles. $\mathrm{Det}(J^*) > 0$ if and only if $(\delta_{00}^L + \delta_{01}^H)(\delta_{11}^H + \delta_{00}^L) > \delta_{11}^H(\delta_{10}^L - \delta_{00}^L) + \delta_{00}^L(\delta_{01}^H - \delta_{11}^H)$, which in this special case is equal to

$$\delta_{00}^L > -\delta_{11}^H \tag{S54}$$

by the definition of A. $\mathrm{Tr}(J^*) > 0$ if and only if $\epsilon\alpha < \frac{\delta_{11}^H \delta_{00}^L \left[\delta_{11}^H(\delta_{10}^L - \delta_{00}^L) + \delta_{00}^L(\delta_{01}^H - \delta_{11}^H)\right]}{(\delta_{11}^H + \delta_{00}^L)^3}$ which in this special case is equal to

$$\epsilon\alpha < \frac{\delta_{11}^H \delta_{00}^L(\delta_{01}^H - \delta_{00}^L)}{(\delta_{11}^H + \delta_{00}^L)^2} \tag{S55}$$

Now That the analysis has been done for the general case under the assumption that $\delta_{11}^H - \delta_{01}^H + \delta_{10}^L - \delta_{00}^L = 0$, we can apply it to the model of Rand et al. (2017).

S3.2 Application to Rand et al. model

In the transformed version of the Rand et al. (2017) minimal model we had

$$\delta_{11}^H = 1 - c - w$$
$$\delta_{01}^H = 1 - c$$
$$\delta_{10}^L = c + w$$
$$\delta_{00}^L = c$$

which can be applied to the conditions for an unstable interior equilibrium in equations S55 and S54. An unstable interior equilibrium occurs when

$$w < 1$$

and

$$\tau_P > \frac{(1-w)^2}{cw(1-c-w)}. \tag{S56}$$

The first condition is satisfied by the assumption needed for the existence of an interior equilibrium, $w + c < 1$ and the assumption that $c \geq 0$ and $w \geq 0$. Notice that when $w = 0$, there does not exist a τ_p for which the interior equilibrium is unstable. This can be seen directly from a necessary condition for cycles, violating equation S18 which requires $w > 0$ (this is from the renewable resource case, but an identical necessary condition exists in the decaying resource case).

S4 Common-pool resource harvesting

Here, we consider a classic model of common-pool resource harvesting. We assume that individuals either harvest with high, e_H, or low, e_L, effort. We let the evolutionary process be governed by a profit function, $\pi(e_i, \eta)$, that maps the resource level and harvest effort into fitness. As before, we assume that the resource, η is governed by logistic growth, and the harvest rate is proportional to η and effort. We can write our system as

$$\epsilon\dot{x} = x(1-x)\left(\pi(e_L,\eta) - \pi(e_H,\eta)\right) \tag{S57a}$$
$$\dot{\eta} = r\eta\left(1 - \frac{\eta}{k}\right) - q\eta\left(xe_L + (1-x)e_H\right), \tag{S57b}$$

where x is the fraction of the population that harvests with low effort, k is the carrying capacity of the resource, q is the efficiency with which effort is transformed into harvest, and

ϵ controls the relative timescales of strategy and resource dynamics. For small ϵ, strategy dynamics are fast relative to resource dynamics.

Now, we turn our attention the the profit function, $\pi(e_i, \eta)$. In this simplest case, revenue will depend on the harvest and the price at which the harvested resource can be sold, and costs will increase linearly in effort. Under these assumptions, we can write the profit of an individual as

$$\pi(e_i, \eta) = pq\eta e_i - we_i \tag{S58}$$

where p is the fixed price of the resource and w is the marginal cost of effort.

This gives us a complete description of our system, however, it is not immediately obvious that this model is a special case of the renewable resource case studied in detail above. Employing this profit function, we can simply express our system of equations as

$$\epsilon\dot{x} = x(1-x)(e_H - e_L)(w - pq\eta) \tag{S59a}$$

$$\dot{\eta} = r\eta\left(1 - \frac{\eta}{k}\right) - q\eta\left(xe_L + (1-x)e_H\right). \tag{S59b}$$

Throughout this analysis, We assume that $e_L < e_H$. Now, in order to make an exact mapping between this model and the general renewable resource model analyzed in section 2.1 we linearly transform the resource level, η, into an environmental metric, n that is bounded between 0 and 1. Within this transformed space, we can construct a payoff matrix, $\Pi(n)$ that maps onto our common-pool resource harvesting case.

First, we define our environmental metric as

$$n = \frac{\eta - k\left(1 - \frac{qe_h}{r}\right)}{(e_H - e_L)\frac{qk}{r}}$$

and write the state of our resulting system in terms of x and n. We have

$$\epsilon\dot{x} = x(1-x)(e_H - e_L)\left(w + pqk\left(1 - \frac{qe_H}{r}\right) - \frac{pq^2k}{r}(e_H - e_L)n\right) \tag{S60a}$$

$$\dot{n} = \left(r - q(e_L n + e_H(1-n))\right)(x - n). \tag{S60b}$$

From this we can reconstruct a payoff matrix $\Pi(n)$ that leads to this system equations. The

entries of $\Pi(n)$ are

$$R_0 = S_0 = \left[pqk\left(1 - \frac{qe_H}{r}\right) - w\right] e_L \tag{S61a}$$

$$T_0 = P_0 = \left[pqk\left(1 - \frac{qe_H}{r}\right) - w\right] e_H \tag{S61b}$$

$$R_1 = S_1 = \left[pqk\left(1 - \frac{qe_L}{r}\right) - w\right] e_L \tag{S61c}$$

$$T_1 = P_1 = \left[pqk\left(1 - \frac{qe_L}{r}\right) - w\right] e_H. \tag{S61d}$$

Thus, we can write the values of δ as

$$\delta_{11}^H = \delta_{01}^H = \left[pqk\left(1 - \frac{qe_L}{r}\right) - w\right](e_H - e_L) \tag{S62a}$$

$$\delta_{00}^L = \delta_{10}^L = -\left[pqk\left(1 - \frac{qe_H}{r}\right) - w\right](e_H - e_L). \tag{S62b}$$

Depending on the parameter values chosen we have three possible outcomes. First, when positive profits occur at the low effort dominated environmental equilibrium but negative profits result at the high impact dominated equilibrium then we have $\delta_{11}^H = \delta_{01}^H > 0$ and $\delta_{00}^L = \delta_{10}^L > 0$. This implies that the system always falls at the boundary of the region where cycles are possible in Figure 2b. This implies that while cycles cannot occur in this system, small changes to the payoff structure could lead to cycles. In particular, holding all else equal, increasing δ_{01}^H or δ_{10}^L would permit cycles.

Second, if e_H is low enough that $pqk\left(1 - \frac{qe_H}{r}\right) - w > 0$, then $\delta_{00}^L = \delta_{10}^L < 0$ and the other δ's will be positive. Thus, by referencing figure 2d, we conclude that the only stable outcome is the high-impact equilibrium. Third, if both $pqk\left(1 - \frac{qe_H}{r}\right) - w < 0$ and $pqk\left(1 - \frac{qe_L}{r}\right) - w < 0$, then we have $\delta_{00}^L = \delta_{10}^L > 0$ and $\delta_{11}^H = \delta_{01}^H < 0$. As illustrated in figure 2c, this implies that the low impact dominated state will be the equilibrium outcome. We assumed ex-ante that $e_L < e_H$ and thus these are the only possible outcomes within this system.

S5 Market pricing CPR model

While the simplest common-pool resource harvesting model cannot produce cyclic dynamics, one possible driver could be market pricing. Whereas in the previous section the price received for each unit of harvested resource was constant, here we let the price received be a function of the total harvest at the present time, to mimic market pricing. A fixed price makes sense in the case where the system in question represents a small part of a large or global market because then local supply can have only a small impact on the global market price. Here, we allow harvest quantity to effect the price. This is more applicable to cases

where the markets for the resource are local or the suppliers in consideration account for a significant portion of total supply. As a first approximation, we assume that the market price is linearly decreasing in the quantity supplied.

This alters that profit function, resulting in

$$\pi(e_i, x, n) = p(h)qne_i - we_i \tag{S63}$$

where $h = nq(xe_L + (1-x)e_H)$ and $p(h)$ is the market price as a function of resource supply. This model is not a special case of the model presented in section 2.1 since there are higher order terms in the dynamical equations introduced through the dependency of the price of the resource on the state of the system. We consider the linear price equation,

$$p(h) = p_0(1 - \gamma h)$$

so that there is a price ceiling of p_0 and a linear decrease with slope γ as supply increases. With this formulation, we can write the profit of low and high effort harvesters as

$$\begin{aligned}\pi_L(x, n) &= p_0(1 - \gamma nq(xe_L + (1-x)e_H))qne_L - we_L \\ \pi_H(x, n) &= p_0(1 - \gamma nq(xe_L + (1-x)e_H))qne_H - we_H.\end{aligned}$$

In total, the model can be written as

$$\epsilon\dot{x} = x(1-x)\left(\pi_L(x, n) - \pi_H(x, n)\right) \tag{S64a}$$

$$\dot{n} = rn\left(1 - \frac{n}{k}\right) - qn\left(xe_L + (1-x)e_H\right). \tag{S64b}$$

Bifurcation analysis allows us to show how equilibria (and their stability) change as a function of key parameters of interest. First, we examine the effect of price elasticity on the equilibrium fraction of low-effort harvesters. Price elasticity, γ, is a measure of how quickly price declines as supply increases. The equilibrium state of the resource can also be displayed, however, in our model there is a linear relationship between the fraction of low-effort harvesters and the equilibrium state of the resource. Thus, we only present the bifurcation diagram in the fraction of low-effort harvesters, x. Figure S1a shows that under regime with a high maximum price, p_0, increasing the rate at which harvest quantity depresses market price, γ, leads to hysteresis and multiple stable states. On the other hand, figure S1b shows that under a low maximum price, increasing γ leads to a smooth transition from one equilibrium to the other, without a region of multiple stable states.

S5.1 Market pricing analysis

The interior strategy nullcline of the system changes from previous models because market pricing of harvest changes the set of points where zero profits result. Letting $\pi(e_L, x, n) - \pi(e_H, x, n) = 0$ and solving for n gives

$$n = \frac{p_0 \pm \sqrt{p_0(p_0 - 4\gamma w(xe_L + (1-x)e_H)}}{2p_0\gamma q(xe_L + (1-x)e_H)} \tag{S65}$$

so that there are two branches of the relationship depending on whether the square root is added or subtracted from the relationship. This can be simplified to

$$n = \frac{2w}{p_0 q \pm \sqrt{p_0} q\sqrt{p_0 - 4\gamma w(e_H(1-x) + e_L x)}} \tag{S66}$$

which, since $e_H > e_L$, illustrates that as x increases, the second term in the denominator also increases. This implies that on the upper branch of the nullcline is increasing in x and the lower branch of the nullcline is decreasing in x for all $x \in [0, 1]$, given that $p_0 > 4\gamma w(e_H(1-x) + e_L x)$. This will simplify stability analyses at interior equilibria.

Now we characterize the stability of the equilibria of the system. First, we will consider the interior equilibria.

Interior equilibria At interior equilibria, the environmental nullcline intersects with the strategy nullcline. The analysis will depend on the relative slopes of these nullclines, and whether the intersection occurs at the upper or lower branch of the strategy nullcline. Consider the Jacobian matrix

$$J = \begin{bmatrix} \frac{\partial \dot{x}}{\partial x} & \frac{\partial \dot{x}}{\partial n} \\ \frac{\partial \dot{n}}{\partial x} & \frac{\partial \dot{n}}{\partial n} \end{bmatrix}_{(x^*, n^*)}$$

at the lower branch of the strategy nullcline. We know that the environment nullcline is increasing in x because $e_L < e_H$, and that $\dot{n} > 0$ below the nullcline. Further, from the form of the strategy nullcline, we know that the lower branch is decreasing in x and that $\dot{x} > 0$ below the nullcline. From this we can determine the sign of each element of the Jacobian matrix. In this case we have

$$J = \begin{bmatrix} - & - \\ + & - \end{bmatrix}$$

for the signs of the Jacobian, which implies stability.

Along the upper branch of the nullcline, the stability analysis is slightly more complex. Consider the path derivatives along the $\dot{x} = 0$ and $\dot{n} = 0$ nullclines. By construction, the

value of the path derivative is equal to zero, thus we can write

$$\frac{\partial \dot{x}}{\partial n}\frac{\partial n}{\partial x} + \frac{\partial \dot{x}}{\partial x} = 0$$

for the path derivative along the strategy nullcline where the slope of the nullcline is $\frac{\partial n}{\partial x}$. Similarly, we can write the value of the path derivative along the environment nullcline as

$$\frac{\partial \dot{n}}{\partial n}\frac{\partial n}{\partial x} + \frac{\partial \dot{n}}{\partial x} = 0.$$

Let S_x and S_n denote the slopes of the strategy and environment nullclines at equilibirum, respectively. Using these identities, we can rewrite our Jacobian as

$$J = \begin{bmatrix} -\frac{\partial \dot{x}}{\partial n} S_x & \frac{\partial \dot{x}}{\partial n} \\ -\frac{\partial \dot{n}}{\partial n} S_n & \frac{\partial \dot{n}}{\partial n} \end{bmatrix}_{(x^*, n^*)}$$

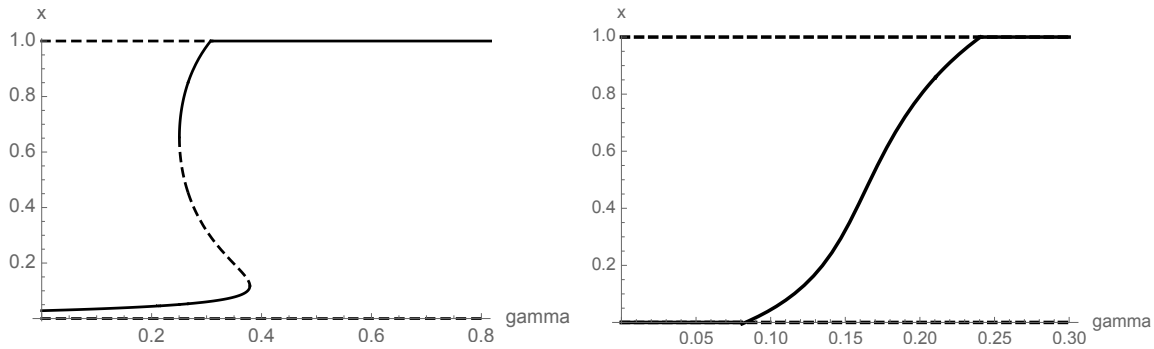
since S_n is positive and $\dot{n} > 0$ below the environment nullcline then $\frac{\partial \dot{n}}{\partial n}(x^*, n^*) < 0$. Also, since S_x is positive and $\dot{x} > 0$ above the upper branch of the strategy nullcline, then we can conclude that $\frac{\partial \dot{x}}{\partial n}(x^*, n^*) > 0$. In total, this implies that $\mathrm{Tr}(J) < 0$ and

$$\mathrm{Det}(J) = \frac{\partial \dot{n}}{\partial n}\frac{\partial \dot{x}}{\partial n}\left(S_n - S_x\right). \tag{S67}$$

We can conclude that the interior equilibrium at an intersection of the upper branch of the strategy nullcline with the environment nullcline will be stable if and only if $S_x > S_n$. If the slope of the environment nullcline is greater than the strategy nullcline, then the interior equilibrium at this point will be a saddle. Note that never does the stability of an interior equilibrium depend on the relative timescale of resource and strategy dynamics, ϵ.

Edge equilibria Here, we analyze the stability of the equilibria at the edge of the phase space. These analyses are simplest graphically. Figure S2 highlights 8 qualitatively different phase diagrams that can result from this system. Given that $e_L < e_H$ and e_L is low enough that it will not drive the environment to zero, then both equilibria at $n = 0$ will be unstable. The equilibrium at $x = 0$ and $n > 0$ is stable if and only if it's location falls above the lower branch of the strategy nullcline, but below the upper branch of the strategy nullcline. Conversely, the equilibrium at $x = 0$ and $n > 0$ is stable if and only if its location falls below the lower, or above the upper branch of the strategy nullcline.

Figure S2 shows a panel of possible outcomes of our model of market pricing, harvest and environmental dynamics. While there are many possible qualitative outcomes, none involve



(a) High p_0 (b) Low p_0

Figure S1: Bifurcation diagrams under high and low price regimes showing multiple equilibria and hysteresis in γ under a high p_0 and a smooth transition from high-effort dominance to low effort dominance under a low p_0 regime.

cyclic dynamics.

S6 Frequency dependent harvesting efficiency CPR model

In this section we extend the common-pool resource model introduced in section 3.3 with the addition of a term to account for the dependency of harvest efficiency, q, on the frequency of a strategy. This model is not a special case of the general renewable resource model outlined in section (2.1) because the frequency dependent harvest efficiency terms alter the dynamics of the resource. The payoff function, however, is a special case of the payoff matricies considered in section (2.1). Suppose that low effort harvesters share information about the state of and location of the resource. This could lead to increasing harvest efficiency, q, as a function of the fraction of the population who harvest with low effort, x. Alternatively, each strategy may require specialized skills and labor. As a strategy increases in frequency, the supply of these skills increases, potentially leading to efficiency gains. In figure 5 dynamics are shown for the case that only low effort harvesters have efficiency that increases in their frequency. This can lead to limit cycles depending on the relative speed of the resource dynamics. We formalize this by considering a catchability function, $q(x)$ that increases linearly in x for low effort harvesters, and decreases in x for high effort harvesters. This indicates that when a particular strategy is more common, the harvest of the resource by players with that strategy becomes more efficient. This could result form communication about the location of the resource, which would lead to an increase in harvest per unit effort for a given environmental state.

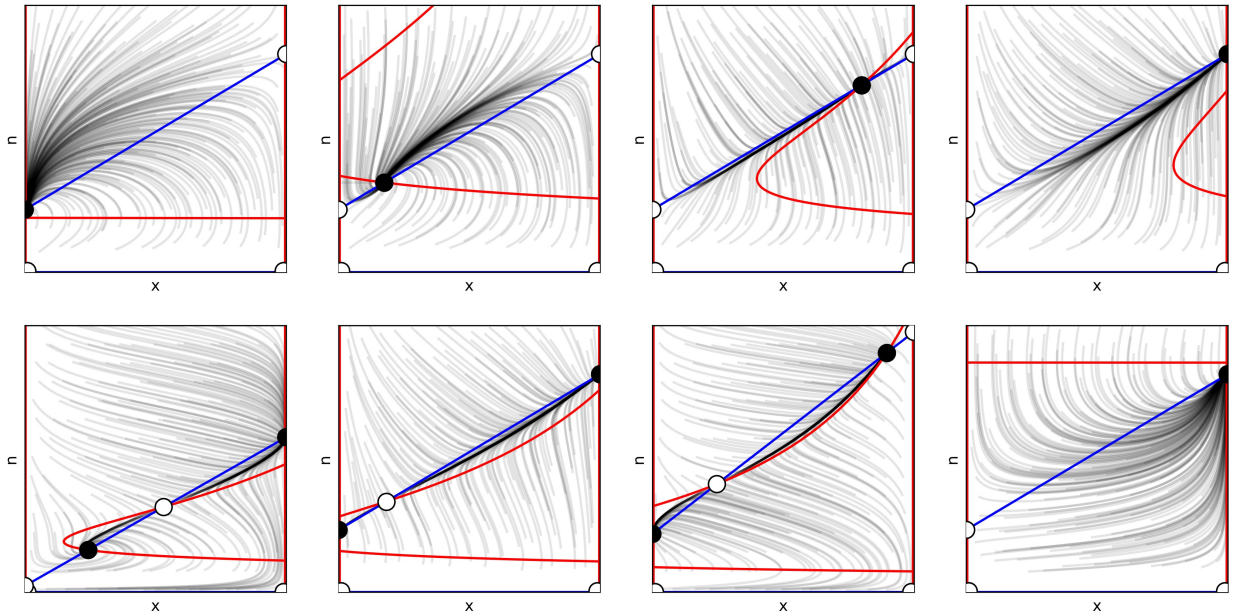


Figure S2: Phase planes under eight qualitatively distinct scenarios. Red curves are strategy nullclines, where $\dot{x} = 0$. Blue lines are environment nullclines, where $\dot{n} = 0$. Equilibria are marked with circles, and occur at intersections of the strategy and environment nullclines. Open circles correspond to unstable equilibria, and closed circles correspond to stable equilibria.

Specifically, we extend the basic model of section 3.3 by incorporating frequency dependent catchability. For low effort harvesters, we let $q_L(x) = q_0(1 + \alpha_L x)$ and for high effort harvesters we let $q_H(x) = q_0(1 + \alpha_H(1 - x))$ such that, all else being equal, harvest rates increase with increase prevalence of a strategy, and the magnitude of the benefit of increased frequency is controlled by α_L and α_H. The profit of each strategy can be written as

$$\pi_L(x, n) = pq_0(1 + \alpha_L x)ne_L - we_L \tag{S68a}$$

$$\pi_H(x, n) = pq_0(1 + \alpha_H(1 - x))ne_H - we_H \tag{S68b}$$

With these modifications, our system can be written as

$$x' = x(1 - x)\left(pnq_0(e_L(1 + \alpha_L x) - e_H(1 + \alpha_H(1 - x))) - w(e_L - e_H)\right) \tag{S69a}$$

$$n' = \epsilon rn\left(1 - \frac{n}{k}\right) - \epsilon q_0 n\left(e_L x(1 + \alpha_L x) + e_H(1 - x)(1 + \alpha_H(1 - x))\right), \tag{S69b}$$

given that time has been re-scaled.

To analyze this system we consider the nullclines. The sets of points where $n' = 0$ are $n = 0$ and

$$n = k\left(1 - \frac{q_0}{r}(e_L x(1 + \alpha_L x) + e_H(1 - x)(1 + \alpha_H(1 - x)))\right). \tag{S70}$$

The sets of points where $x' = 0$ are $x = 0$, $x = 1$ and

$$n = \frac{w(e_H - e_L)}{pq_0\left[(e_H + e_H\alpha_H - e_L) - (e_H\alpha_H + e_L\alpha_L)x\right]}. \tag{S71}$$

Since $e_H > e_L$ we know that the strategy nullcline is increasing in x when the strategy nullcline lies within the state space, $n > 0$. Further, the resource nullcline is quadratic in x and opens downward. We are in particular interested in the stability of interior equilibria. Stability at interior equilibria depends on the relative timescale of resource and strategy dynamics, as well as on the slopes of the nullclines. Consider the path derivatives of the resource and strategy dynamics equations along their respective nullclines, which are equal to zero, by construction. This allows us to write the Jacobian Matrix as

$$J = \begin{bmatrix} -\frac{\partial x'}{\partial n}S_x & \frac{\partial x'}{\partial n} \\ -\frac{\partial n'}{\partial n}S_n & \frac{\partial n'}{\partial n} \end{bmatrix}_{(x^*, n^*)}.$$

Stability at the equilibrium can be determined from the trace and determinant of J. We have

$$\mathrm{Det}(J) = \frac{\partial n'}{\partial n}\frac{\partial x'}{\partial n}\left(S_n - S_x\right). \tag{S72}$$

The structure of our system guarantees that $\frac{\partial n'}{\partial n}$ and $\frac{\partial x'}{\partial n}$ will be negative at equilibrium. Therefore, $S_n > S_x$ is necessary, but not sufficient for stability. If $S_x > S_n$ the interior equilibrium will be a saddle. Given that $S_n > S_x$, then stability will occur when when the trace of J is negative. Due to our separation of timescales, we have a term, ϵ, that controls the relative speed of resource dynamics. We have

$$\mathrm{Tr}(J) = \frac{\partial n'}{\partial n} + \frac{\partial x'}{\partial x} \tag{S73}$$

with $\frac{\partial n'}{\partial n} < 0$ and $\frac{\partial x'}{\partial x} > 0$. Since the first term contains ϵ, we know that the trace will be negative, and stability will result for sufficiently fast resource dynamics (large ϵ) and conversely the equilibrium will be unstable for slow resource dynamics.

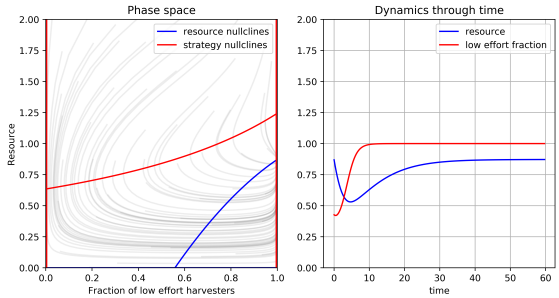
While we can solve for the critical value of ϵ that separates parameter regions leading to stability with those leading to an unstable equilibrium and a limit-cycle, the closed form solution is unwieldy and does not enhance understanding. However, we can use this expression to quickly find the critical value of ϵ for any set of parameter values.

Changes in r, the intrinsic rate of growth of the resource, not only change the speed of resource dynamics, but also the location and stability of the equilibria of the system. For low r, corresponding to resources with low productivity, only low effort harvesting is stable. As r increases high effort harvesters can be supported at equilibrium, but this equilibrium is in close proximity to the low effort dominated equilibrium which is no longer stable, but only just so. Intuitively, this makes limit cycles less likely to occur because dynamics pass near two equilibria, slowing strategy dynamics and limiting environmental overshoot that drives cyclic dynamics. As a result, limit cycles occur for larger values of ϵ when the interior equilibrium is near the center of the state space. This highlights the non-monotonicity of the critical value of ϵ in r. For a fixed value of ϵ, increasing r can destabilize, then stabilize the system (see Figure S3).

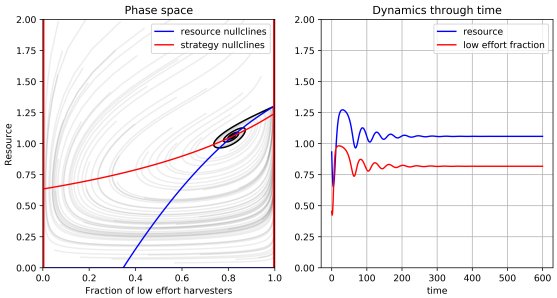
As α_L and α_H get larger, the strength of positive frequency dependence increases. This can lead to sets of nullclines that cross twice in the interior of the state space. At the intersection where the resource nullcline has a greater slope than the strategy nullcline stability depends on ϵ, as before. The other interior equilibrium will be a saddle, and one of the edge equilibria will be stable. This can lead to three outcomes. First, if both the interior and edge equilibrium ate stable, then there will be dependence on initial conditions with dynamics either leading to the interior or edge equilibrium. Next, if ϵ is small, the interior equilibrium becomes unstable and a limit cycle forms around it due to a Hopf bifurcation. In this case there is still dependence on initial conditions where either a limit cycle or an edge equilibrium result. Finally, if ϵ is too small, the interior equilibrium is unstable and no

limit cycle results, all initial conditions lead to the edge equilibrium.

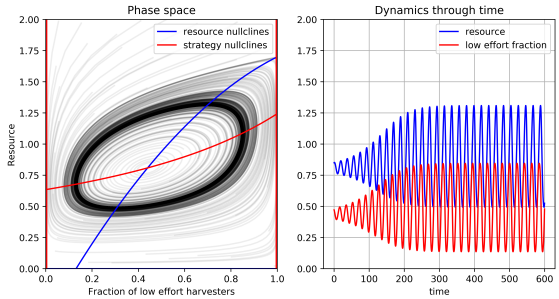
To illustrate this complexity, we consider a range of cases with where only r changes. When we let $\epsilon = 2.1$, increasing r can first de-stabilize the interior equilibrium, then stabilize it. This highlights the non-monotonicity of the critical value of ϵ in r. Figure S3 shows that intermediate values of r can lead to cyclic dynamics. This is in contrast to the stability condition under the renewable resource model where we found that both r and ϵ had similar effects of stability.



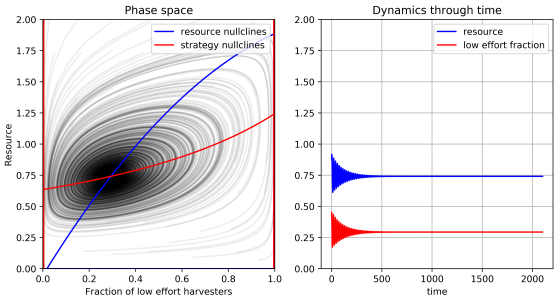
(a) Dynamics for $r = .25$



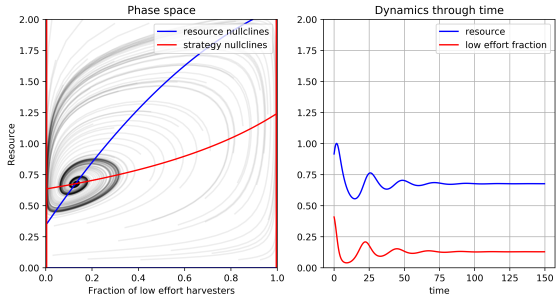
(b) Dynamics for $r = .29$



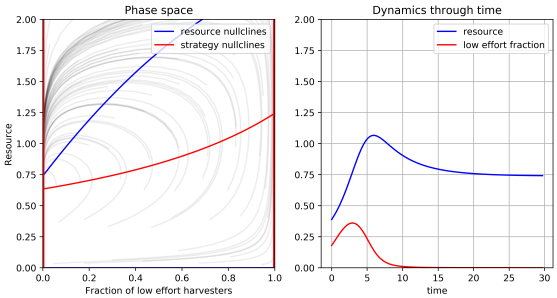
(c) Dynamics for $r = .34$



(d) Dynamics for $r = .37$



(e) Dynamics for $r = .41$



(f) Dynamics for $r = .46$

Figure S3: As r, the intrinsic rate of growth of the resource, increases, the speed of resource dynamics increase and the location of the equilibria change. As opposed to changes in ϵ where higher values always stabilize an interior equilibrium, increasing r can either stabilize or de-stabilize an interior equilibrium depending on context. Here we show that all else being equal, increase r can lead from stable equilibria, to cycles and back.