Ecosystem Management in Models of Antagonistic Species Coevolution

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1 Introduction

Antagonistic coevolution of species and pests or parasites can be described by the so-called "Red Queen" hypothesis.[1] According to this hypothesis, parasites evolve ceaselessly in response to perpetual evolution of species' (or hosts') resistance. The coevolution of the parasites' ability to attack (virulence) and the hosts' resistance is expected to indicate persistent fluctuations of resistance and virulence. In this context the Red Queen hypothesis generates a continuous need for variation, and a common clone will be wiped out by parasites that have adapted to parasitize it.

In coevolutionary models the interaction of population (or biomass) dynamics and mutation (or trait dynamics) leads to "Red Queen cycles". A limit cycle or other non-point attractors in trait space dynamics are called "Red Queen" races because, for example, in predator-prey systems each is evolving its trait against the other and the traits are moving dynamically, unlike a fixed point. Red Queen cycles are observed in a slow time scale, since trait dynamics are assumed to evolve slowly, in contrast to the population, host - parasite, dynamics which are assumed to evolve fast.[2] Thus the analy-

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[1]See, for example, van Valen (1973) and Kawecki (1998).
[2]See Dieckmann and Law (1996) and Marrow, Dieckmann and Law (1996).

sis of antagonistic coevolution of species can be formally analyzed in a fast - slow time framework, by using results from singular perturbation analysis, since there is a time scale separation of population dynamics, which evolve in fast time scale, and evolution which takes place in slow time scale. A central question in this context is whether mutation, that is trait dynamics, evolve slow but not that slow to make the analysis of mutation dynamics redundant for policy purposes. If mutation is redundant because it operates very slowly, then it is the analysis of population dynamics which is important. This is of course an empirical issue, however there are indications related to resistance development for genetically modified crops in agriculture, or to resistance development to antibiotics that suggest that the slow movement of mutation might be relevant and important in certain cases for analyzing the whole system and for developing sensible policies. For example in ecosystem management models, management decisions leading to a less diverse group of species, or hosts, could increase the effectiveness of pests in attacking the less diverse group of species and disrupt the "Red Queen" races.[3]

The purpose of our paper is to develop a unified ecological/economic conceptual framework for ecosystem management, which takes into account population, and trait dynamics characterizing antagonistic coevolution. Population dynamics evolve in fast time, while trait dynamics evolve in slow time. We seek to explore the outcome of management rules seeking to provide a conceptual framework to answer questions such as: How is human management affecting Red Queen races? Can human management remove a non-point attractor in trait space dynamics? What will be the effect on the value of an ecosystem, the value defined in terms of the Bellman state valuation function, if management decisions ignore the underlying mutation and trait dynamics? How can ecosystem sustainability criteria be defined in the context of a coevolutionary model?

The time scale separation in the analysis of coevolutionary models introduced in this paper might be useful in providing a conceptual framework

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[3]There are empirical studies documenting the presence of genetic variation for resistance against plant pathogens or against animal parasites. See, for example, H. J. Carius et al. (2001), or Lively and Dybdahl (2000) for an empirical verification of the Red Queen hypothesis for fresh water snails in New Zealand.

capable of detecting discrepancies, between the perceived evolution of ecosystems under management that ignores certain slow state variables and treats them as fixed, and the actual evolution of the ecosystem when the slow state variables actually evolve and move the system in a certain direction, which might not be a desirable one. These discrepancies might be a cause for *surprises* in ecosystem management. For example profit-maximizing decisions which ignore evolution might steer the system to a certain steady state on a fast time scale, but then the underlying trait dynamics might move the system in slow time to another attractor. How can we provide a measure of the relative change in the value of the ecosystem,[4] between the perceived steady state under profit maximizing in fast time, and the actual steady state to which the system is expected to converge eventually, under population dynamics and evolution? Since steady-state species diversity under profit maximization in fast time may very well differ from the corresponding diversity when full optimization is carried out, the measure of relative change in ecosystem's valuation could provide a measure for valuing changes in biodiversity. This result in a sense complements and extends the result of Brock and Xepapadeas (2004) about biodiversity valuation through the Bellman state valuation function, to the multi-species case with antagonistic coevolution.

An associated issue that we also seek to tackle in this paper is whether we can use this analytical framework to develop sustainability criteria for an ecosystem based on the "non declining value" concept of sustainability.[5] In this context we define sustainability criteria under full optimization where population dynamics and evolution are taken into account, and for the case where evolution is ignored. This type of analytical approach might help explore the question of whether ignorance of evolutionary forces in designing management rules might lead to nonsustainable paths.

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[4]It should be noted that the valuation of the ecosystem is based on the present value of the flow of benefits that humans derive from the system. This flow of benefits could be defined in a broad way to involve benefits from harvesting species, but also benefits from existence values associated with species biomasses. (see for example Brock and Xepapadeas 2002).

[5]See Arrow, Dasgupta and Maler (2003), Pemberton and Ulph (2001).

The rest of the paper is organized as follows: Section 2 develops the coevolutionary model for one harvested species-one pathogen, sets up the fast-slow time framework, and compares harvesting rules that ignore the slowly evolving mutation, with the optimal harvesting rule that takes into account fast and slow state variables. We derive sufficient conditions under which human management might disrupt Red Queen races. Section 3 generalizes to a many species-many pathogens framework and provides a conceptual framework under which the Bellman state valuation function of the coevolutionary model can be used to value changes in the ecosystems diversity. Section 4 develops ecosystem sustainability criteria, and section 5 concludes.

2   Harvesting and coevolution: One species - one pathogen

We first consider human management in the form of harvesting in a system with one harvested ("useful") species or host species whose biomass is denoted by x and a parasite denoted by y, where the abundance of x and y depends on the evolution of two characteristics or traits denoted by d and γ, [6] where d affects the fitness of x and γ affects the fitness of y.

Let the growth rates of x and the pathogen y be given, similar to Krakauer and Jansen (2002), by

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\begin{aligned}
g_x &= \frac{\dot{x}}{x} = (s - rx - yQ(d, \gamma)) \\
g_y &= \frac{\dot{y}}{y} = (xQ(d, \gamma) - \delta)
\end{aligned}
$$

then $\frac{\partial g_x}{\partial d} = -y \frac{\partial Q(d,\gamma)}{\partial d}$ and $\frac{\partial g_y}{\partial \gamma} = x \frac{\partial Q(d,\gamma)}{\partial \gamma}$. If we measure fitness by growth rates then $\frac{\partial Q(d,\gamma)}{\partial d} < 0$ so that an increase in d increases fitness of x. In the same way $\frac{\partial Q(d,\gamma)}{\partial \gamma} > 0$ for an increase in γ to increase fitness of y. Then in

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[6]This approach essentially adds a management dimension, in the form of harvesting one species, to Red Queen dynamic models developed by Krakauer and Jansen (2002).

equilibrium where $\dot{x} = \dot{y} = 0$, we have, for any fixed values of traits d and γ :

$$\hat{x} = \frac{\delta}{Q\left(d,\gamma\right)} \ , \ \hat{y} = \frac{s - r\hat{x}}{Q\left(d,\gamma\right)} \ , s \geq r\hat{x}$$

Assume that species x is harvested, with harvest at each point in time given by $h = qEx$, where E denotes effort and q is the usual catchability coefficient. Then the evolution of x and y is given by:

$$\dot{x} = x\left(s - rx - yQ\left(d,\gamma\right)\right) - qEx \tag{1}$$

$$\dot{y} = y\left(xQ\left(d,\gamma\right) - \delta\right) \tag{2}$$

For any fixed effort $\tilde{E}$ and fixed trait values the equilibrium (steady state) for the two populations is defined as

$$\tilde{x} = \frac{\delta}{Q\left(d,\gamma\right)} \ , \ \tilde{y} = \frac{s - r\tilde{x} - q\tilde{E}}{Q\left(d,\gamma\right)} \ , s \geq r\tilde{x} + q\tilde{E} \tag{3}$$

For a non negative steady state $(\tilde{x}, \tilde{y})$ the Jacobian of (1), (2) is defined as

$$J_{xy} = \begin{pmatrix} -r\tilde{x} & -\tilde{x}Q\left(d,\gamma\right) \\ \tilde{y}Q\left(d,\gamma\right) & 0 \end{pmatrix} \tag{4}$$

Since $\mathrm{tr}J < 0$ and $\det J > 0$ the steady state $(\tilde{x}, \tilde{y})$ is asymptotically stable. The following result can be stated:

Result 1: *For any fixed effort level and fixed trait values, the steady state of the host-parasite populations entailing positive abundances is asymptotically stable*

Assuming constant mutation rates μ_d and μ_γ the evolutionary dynamics for the traits d and γ, when population dynamics have reached the asymp-

totically stable steady state, in the no harvesting case, are given by[7]

$$\dot{d} = -\mu_d \hat{x} \hat{y} \frac{\partial Q(d, \gamma)}{\partial d} \qquad (5)$$

$$\dot{\gamma} = \mu_\gamma \hat{x} \hat{y} \frac{\partial Q(d, \gamma)}{\partial \gamma} \qquad (6)$$

2.1 Evolutionary dynamics in a fast time - slow time framework

A coevolutionary model under harvesting can be developed by combining the population dynamics (1), (2) with trait dynamics. In developing this model of coevolution we explicitly introduce two time scales. Population dynamics move fast, while mutation, that is trait dynamics move slow.[8] Thus the whole dynamic system that includes the host species, the parasite and mutation can be written as:

$$\varepsilon \dot{x} = x \left(s - rx - yQ(d, \gamma) \right) - qEx \ , x(0) = x_0 \qquad (7)$$

$$\varepsilon \dot{y} = y \left(xQ(d, \gamma) - \delta \right) \ , y(0) = y_0 \qquad (8)$$

$$\dot{d} = -\mu_d xy \frac{\partial Q(d, \gamma)}{\partial d} \ , d(0) = d_0 \qquad (9)$$

$$\dot{\gamma} = \mu_\gamma xy \frac{\partial Q(d, \gamma)}{\partial \gamma} \ , \gamma(0) = \gamma_0 \qquad (10)$$

where the small positive parameter ε indicates the fact that the host - parasite biomasses evolve faster than mutation. At the limit $\varepsilon \to 0$ and the dynamic system for the host, the parasite and mutation (7) - (10) is reduced to a set of two algebraic and two differential equations. The set

$$M = \{(x, y; d, \gamma) : x \left(s - rx - yQ(d, \gamma) \right) - qEx = 0, y \left(xQ(d, \gamma) - \delta \right) = 0\} \qquad (11)$$

is a two-dimensional manifold and (9), (10) represents a dynamical system on M. Solving (7), (8) for x and y, the manifold M can be locally parametrized by x and y for any effort level E, and we can obtain the abundances for x

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[7]See Krakauer and Jansen (2002).

[8]See Dieckmann and Law (1966) and Marrow, Dieckmann and Law (1966).

and y which converge fast to their equilibrium values

$$\hat{x} = \hat{x}\left(d, \gamma\right) = \begin{cases} 0 \text{ or} \\ \frac{\delta}{Q(d,\gamma)} \end{cases} , \ \hat{y} = \hat{y}\left(d, \gamma, E\right) = \begin{cases} 0 \text{ or} \\ \frac{s-r\hat{x}-qE}{Q(d,\gamma)}, s > r\hat{x} + qE \end{cases} \quad (12)$$

Then, mutation evolves in slow time according to *reduced system* or *slow time scale system*:

$$\dot{d} = -\mu_d \hat{x}\left(d, \gamma, E\right) \hat{y}\left(d, \gamma, E\right) \frac{\partial Q\left(d, \gamma\right)}{\partial d} \quad (13)$$

$$\dot{\gamma} = \mu_\gamma \hat{x}\left(d, \gamma, E\right) \hat{y}\left(d, \gamma, E\right) \frac{\partial Q\left(d, \gamma\right)}{\partial \gamma} \quad (14)$$

The *fast time scale system* is obtained by rescaling time t to $\tau = t/\varepsilon$. Then the *boundary layer system* is defined as:

$$x' = x\left(s - rx - yQ\left(d, \gamma\right)\right) - qEx \ , x\left(0\right) = x_0 \quad (15)$$

$$y' = y\left(xQ\left(d, \gamma\right) - \delta\right) \ , y\left(0\right) = y_0 \quad (16)$$

$$d' = 0 \ , d\left(0\right) = d_0 \ , \ \gamma' = 0 \ , \ \gamma\left(0\right) = \gamma_0 \quad (17)$$

where $z' \equiv dz/d\tau$, $z = x, y, d, \gamma$ and d and γ are "frozen" at their initial values. The fast time scale system is defined from the boundary layer system with d and γ as fixed parameters. Then M, which is the slow manifold (11) consists of the set equilibria of the fast system. The stable equilibria of the fast system constitute the "attracting" portion of the slow manifold, while the unstable equilibria constitute the "non attracting" portion of the slow manifold.

Assume that population dynamics, the fast time scale system, tend to an asymptotically stable steady state $\hat{x}\left(d, \gamma\right), \hat{y}\left(d, \gamma\right)$. Furthermore, the solution of the boundary layer problem (15) - (17) is defined for all $\tau \geq 0$ and tend to the asymptotically stable equilibrium point $\hat{x}\left(d_0, \gamma_0\right), \hat{y}\left(d_0, \gamma_0\right)$. Thus the fast transition of population dynamics bring the solution of the full problem close to the "attracting" portion of the slow manifold. Then the slow motion of mutation takes place near the slow manifold and can be approximated by the solution of the reduced problem (13) - (14).

It is interesting to note that if the population dynamics are characterized by locally stable and unstable steady states, then mutation, the slow variable, acts as a bifurcation parameter for the dynamics of the frozen boundary layer problem (Sastry 1999). Thus if the steady state of the boundary layer problem is close to the non attracting part of M, then disturbance and noise may cause the state (x, y, d, γ) to "slip" and transit infinitely fast to another attracting portion of M. Thus in this context population dynamics may show jumps from the non attractive parts of M to attractive parts, with mutation acting as a bifurcation parameter.

The approximations of the full system (7) - (10) by the fast and slow systems can be described as follows. Let $x_0(\tau), y_0(\tau)$ be the solution of the boundary layer population problem with $x_0(d, \gamma), y_0(d, \gamma)$ isolated locally stable equilibria. Let $d_0(t), \gamma_0(t)$ be the solution of the slow, mutation, problem, and let d^*, γ^* be asymptotically stable equilibria of the reduced system. As it has been shown in the general context of Tykhonov's theorem (Wasow 1965; Lobry, Sari and Touhami 1998) for $t \in [0, +\infty)$ and for any solution $(x(\varepsilon\tau), y(\varepsilon\tau), d(t), \gamma(t)), \tau = t/\varepsilon$ of the full system (7) - (10) there exist, in some appropriately defined domain, $\delta > 0$ with $\varepsilon > \delta$ such that

$$\|x(\varepsilon\tau) - x_0(\tau)\| \quad < \quad \delta \ , \ \ \|y(\varepsilon\tau) - y_0(\tau)\| < \delta \ , \tau \leq L \ , \ L > 0 \quad (18)$$

$$\|d(t) - d_0(t)\| \quad < \quad \delta \ , \ \ \|\gamma(t) - \gamma_0(t)\| < \delta \quad\quad\quad\quad\quad (19)$$

These conditions imply that the solution of the reduced system can be used to approximate the evolution of mutation, while the solution of the boundary layer problem can be used to approximate the evolution of population dynamics.

This type of time scale decomposition allows us to study decision making in different time scales but also allows us to study, through the interrelationship between the boundary layer and the reduced problem, the impact on mutation of harvesting decisions taken in fast time. If mutation is so slow that we do not consider its evolution important, then the solution corresponds to the solution of the boundary layer problem; if mutation is not so slow then harvesting affects the reduced problem and thus the evolution of

traits. This is of course an empirical issue, however the conceptual framework developed in this paper provides a fairly general approach to the problem.

Furthermore the solution of the full system can be approximated by synthesizing the solution of the fast and the slow problem as:

$$x\left(t,\varepsilon\right) = x_0\left(t\right) + x\left(\tau\right) + \mathcal{O}\left(\varepsilon\right) \tag{20}$$

$$y\left(t,\varepsilon\right) = y_0\left(t\right) + y\left(\tau\right) + \mathcal{O}\left(\varepsilon\right) \tag{21}$$

$$d\left(t,\varepsilon\right) = d_0\left(t\right) + d\left(\tau\right) + \mathcal{O}\left(\varepsilon\right) \tag{22}$$

$$\gamma\left(t,\varepsilon\right) = \gamma_0\left(t\right) + \gamma\left(\tau\right) + \mathcal{O}\left(\varepsilon\right) \tag{23}$$

where $\left(x_0\left(t\right), y_0\left(t\right)\right) = \left(\phi^x\left(d_0\left(t\right), \gamma_0\left(t\right)\right), \phi^y\left(d_0\left(t\right), \gamma_0\left(t\right)\right)\right)$, $\left(d\left(\tau\right), \gamma\left(\tau\right)\right) = \left(d_0, \gamma_0\right)$

Krakauer and Jansen (2002) consider the slow time scale system, for the no human intervention case corresponding to $E = 0$. Using $s = 0$ in the growth of x and $Q\left(d, \gamma\right) = \left(\frac{1-\gamma}{1-(d+\alpha-2d\alpha)} + \frac{\gamma}{1-(d+\alpha-2d\alpha)} + \varepsilon\right)^{-1}$, they show that the equilibrium point for the reduced system $\left(d^*, \gamma^*\right) : \dot{d} = \dot{\gamma} = 0$, is not attracting but the dynamics spiral away from this point. This behavior is the oscillatory, Red Queen, dynamics of the host and parasite population.

By formally introducing different time scales, which allow us to examine the impact of the slow mutation dynamics on the steady state of the system, we seek: (i) to model the impact of harvesting on Red Queen dynamics, and (ii) to define in the context of coevolution the value of the ecosystem at the steady state, with the value defined by the *Bellman state valuation function*. This value concept of the ecosystem can prove useful in discussing biodiversity valuation issues as well as ecosystem *sustainability* issues.

To accomplish this task we examine alternative harvesting rules for the host species x.

Harvesting rules can vary from optimal harvesting where harvesting is chosen to maximize utility from harvesting subject to the full system dynamics (7) - (10), to harvesting rules where optimization might not be an objective or where optimization is taking place but some of the parasite or the trait dynamics are ignored.

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2.2 Maximum Sustainable Yield Rule

We consider first the case where harvesting is taking place according to the maximum sustainable yield (msy) rule and traits are considered as fixed. This approach implies that the problem is solved in *fast time,* where the values of the traits are "frozen" at the initial values (d_0, γ_0). If we rescale time t to $\tau = t/\varepsilon$, then

$$\frac{\partial d}{\partial \tau} = \frac{\partial \gamma}{\partial \tau} = 0 \ , d(0) = d_0 \ , \ \gamma(0) = \gamma_0 \tag{24}$$

$$\frac{\partial x}{\partial \tau} = x(s - rx - yQ(d, \gamma)) - qEx \tag{25}$$

$$\frac{\partial y}{\partial \tau} = y(xQ(d, \gamma) - \delta) \tag{26}$$

Assuming further that at the msy rule that parasite evolution is ignored in the sense that y is treated as a fixed parameter, $\bar{y}$, we have from (25) in equilibrium that

$$x = \frac{s - \bar{y}Q(d_0, \gamma_0) - qE}{r}$$

$$h = qEx = qE\left(\frac{s - \bar{y}Q(d_0, \gamma_0) - qE}{r}\right)$$

Then the msy effort is determined as

$$\hat{E} = \arg\max_{E} qE\left(\frac{s - \bar{y}Q(d_0, \gamma_0) - qE}{r}\right) = \frac{s - \bar{y}Q(d_0, \gamma_0)}{2q} \tag{27}$$

It is clear from (27) that the msy effort is reduced if we take into account the abundance of the parasite, even while ignoring dynamic and considering only "frozen" values. If this abundance is ignored then we have the usual result that $\tilde{E} = s/2q$.

However if harvesting effort is fixed at the $\hat{E}$ level, then using (12) on the slow manifold M given by (11), the realized equilibrium abundances will be

$$\hat{x}_{msy} = \left\{ \begin{array}{c} 0 \text{ or} \\ \frac{\delta}{Q(d_0, \gamma_0)} \end{array} \right. \ , \ \hat{y}_{msy} = \left\{ \begin{array}{c} 0 \text{ or} \\ \frac{s - 2r\hat{x}_{msy} + \bar{y}Q(d_0, \gamma_0)}{Q(d_0, \gamma_0)} \end{array} \right. \tag{28}$$

From **Result 1** the equilibrium entailing positive abundances is asymptotically stable. Then the slow evolution of trait dynamics on the slow manifold is given by:

$$\dot{d} = -\mu_d \hat{x}_{msy} \hat{y}_{msy} \frac{\partial Q(d, \gamma)}{\partial d} = \psi^d(d, \gamma) \tag{29}$$

$$\dot{\gamma} = \mu_\gamma \hat{x}_{msy} \hat{y}_{msy} \frac{\partial Q(d, \gamma)}{\partial \gamma} = \psi^\gamma(d, \gamma) \tag{30}$$

Result 2: *Assume that a steady state* $(d^*, \gamma^*) : \dot{d} = \dot{\gamma} = 0$, *in trait dynamics (29) and (30) exists. Let* J_1 *be the corresponding Jacobian matrix evaluated at* (d^*, γ^*), *and let* D *be a simply connected region containing* (d^*, γ^*) *Then:*

- *if the expression*

$$div(\xi) = \frac{\partial \dot{d}}{\partial d} + \frac{\partial \dot{\gamma}}{\partial \gamma}$$

  does not change sign in D, *then by Bendixon's criterion, no limit cycle can exist in* D.

- *if* $tr(J_1) < 0$ *and* $\Delta = [tr(\mathbf{J}_1)]^2 - 4 \det(J_1) \geq 0$ *the steady state cannot be a focus or a centre.*

  This result provides sufficient conditions for the elimination of red queen cycles. If the slow mutation system converges to the point attractor (d^*, γ^*) then host - parasite populations will converge to the long run equilibrium values $\hat{x}^*_{msy} = \frac{\delta}{Q(d^*, \gamma^*)}, \hat{y}^*_{msy} = \frac{s - 2r\hat{x}^*_{msy}}{Q(d^*, \gamma^*)}, \hat{E}^* = \frac{s - \hat{y}^*_{msy} Q(d^*, \gamma^*)}{2q}$.

2.3 Optimal Harvesting Rules and Ecosystem Valuation

Assume that the flow of benefits from harvesting the species is given by $S(qE(t)x(t)) - cE(t)$, where $S(\cdot)$ is an increasing strictly concave benefit function and c is fixed cost per unit effort. The objective is to choose a path

for effort to maximize discounted net benefits or,

$$\max_{\{E(t)\}} \int_0^\infty e^{-\rho t} \left[S\left(qE\left(t\right)x\left(t\right)\right) - cE\left(t\right) \right] dt \tag{31}$$

We can distinguish a number of cases regarding the constraints involved.

1. The optimization takes into account only the useful species population dynamics, and ignores parasite dynamics and mutation. We call this problem the Private Optimization Management Problem (POMP), because it can be regarded as the problem of a private agent that treats parasite dynamics and mutation as externalities which are ignored.

2. The optimization is carried out in fast time and involves only species-parasite dynamics. The values for the traits are "frozen" at some fixed initial values.

3. The optimization takes into account all dynamic constraints and in addition accounts for the fast-slow variable structure. We call this problem the Social Optimization Management Problem (SOMP), because all externalities are taken into account.

2.3.1   The POMP

The problem can be written as

$$\max_{\{E(t)\}} \int_0^\infty e^{-\rho t} \left[S\left(qE\left(t\right)x\left(t\right)\right) - cE\left(t\right) \right] dt \tag{32}$$
subject to (1) where $, y, d, \gamma$ are fixed parameters

The Hamilton Jacobi Bellman (HJB) equation for the problem, where $V\left(x\right)$ is the value function, is:

$$\rho V\left(x\right) = \max_E \left\{ S\left(qEx\right) - cE + \frac{\partial V}{\partial x} \left[x\left(s - rx - \bar{y}Q\left(d_0, \gamma_0\right)\right) - qEx \right] \right\}$$
$$\tag{33}$$

The feedback optimal effort is determined by

$$\tilde{E} = \tilde{E}\left(x; \bar{y}, \bar{d}, \bar{\gamma}\right) : S'\left(q\tilde{E}x\right)qx - c - q\tilde{E}\frac{\partial V}{\partial x} = 0 \qquad (34)$$

The dynamic programming problem can be solved, either by considering trial solutions for the value function and substituting them into (34) and (33),[9] or by substituting (34) into (33) and then solving the differential equation for the value function.

Once the value function has been determined, then (34) determines the *policy function* $\hat{E} = \hat{E}\left(x; \bar{y}, d_0, \gamma_0\right) = \hat{E}\left(x\right)$, which determines the *optimal* effort for each level of the state variable x given the rest of the parameters. At a locally stable steady state x_f^*, the optimal steady state effort is $\hat{E}_f = \hat{E}\left(x_f^*; \bar{y}, d_0, \gamma_0\right) = \hat{E}\left(x_f^*\right)$.

The policy function can also be obtained if we use the Hamiltonian representation for the problem. The current value Hamiltonian is

$$\mathcal{H} = S\left(qEx\right) - cE + p_x\left(x\left(s - rx - \bar{y}Q\left(d_0, \gamma_0\right)\right) - qEx\right) \qquad (35)$$

where the costate variable p_x reflects the resource's shadow value. As is well known

$$\rho V\left(x\right) = \mathcal{H}^0\left(x, \frac{\partial V}{\partial x}\right) \quad p_x = \frac{\partial V}{\partial x} \qquad (36)$$

$$\mathcal{H}^0\left(x, p_x\right) = \max_E \left\{S\left(qEx\right) - cE + p_x\left[x\left(s - rx - \bar{y}Q\left(d_0, \gamma_0\right)\right) - qEx\right]\right\}$$

where $\mathcal{H}^0$ is the maximized Hamiltonian with optimal effort chosen such that:

$$\tilde{E} = \tilde{E}\left(x, p_x\right) : S'\left(q\tilde{E}x\right)qx - c - qxp_x = 0 \qquad (37)$$

The evolution of the state and the costate variable is obtained by the Modified

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[9]For example, with a linear quadratic problem the value function is quadratic. That is, $V\left(x\right) = a_0 + a_1 x + a_2 x^2$. Standard procedures allow the determination of the coefficients a_0, a_1, a_2 in terms of the parameters of the system. With a power benefit function, the solution for the value function can obtained in the class of the power functions.

Hamiltonian Dynamic System (MHDS)

$$\dot{x} \;=\; \frac{\partial \mathcal{H}^0}{\partial p_x} \tag{38}$$

$$\dot{p}_x \;=\; \rho p_x - \frac{\partial \mathcal{H}^0}{\partial x} \tag{39}$$

A steady state is determined as usual as $(x^*, p_x^*) : (\dot{x}, \dot{p}_x) = 0$. Assume that for the problem (32) such a steady state exists, with the saddle point property which is a common result for these kind of models.[10] A *policy function* $p_x = p_x(x)$ can be obtained from (38), (39) by dividing the two relations to obtain:

$$p_x^{'}(x) = \frac{dp_x}{dx} = \frac{\rho p_x - \frac{\partial \mathcal{H}^0}{\partial x}}{\frac{\partial \mathcal{H}^0}{\partial p_x}} \tag{40}$$

Solving this differential equation with boundary condition (x^*, p_x^*) and using the slope of the stable eigenvector of the steady state as the initial slope of the policy function we can obtain the policy function $p_x = p_x(x)$.[11] Substituting this function into (37) we obtain the policy function in terms of efforts as

$$\hat{E} = \hat{E}(x, p_x(x)) = \hat{E}(x) \tag{41}$$

with $\hat{E}_f = \hat{E}(x_f^*)$ at the fast time steady state

The policy function determines what is perceived as optimal harvesting effort for the POMP. So harvesting is adjusted to changes in x, using (41) without taking into account changes in the population of pathogens y or the traits. However, in reality the host-parasite system evolves under the influence of the parasite dynamics and the slow trait dynamics, which are not taken into account by the POMP. In this case the policy function provides a very useful tool for describing what is expected to happen in reality when harvesting is determined according to the POMP. The host - parasite system

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[10]See, for example, Clark (1990) chapter 5 for details.

[11]This is the time elimination method for determining the policy function Barro and Sala-i-Martin (1995), pp. 488.

evolves according to:

$$\varepsilon\dot{x} = x(s - rx - yQ(d, \gamma)) - q\hat{E}(x)x \quad (42)$$

$$\varepsilon\dot{y} = y(xQ(d, \gamma) - \delta) \quad (43)$$

In this case the actual equilibrium values for x and y, assuming positive abundance in equilibrium, determine the slow manifold and are given by:

$$\hat{x}_a = \hat{x}_a(d, \gamma) = \frac{\delta}{Q(d, \gamma)} \ , \ \hat{y}_a = \hat{y}_a(d, \gamma) = \frac{s - r\hat{x} - q\hat{E}(\hat{x}_a)}{Q(d, \gamma)} \quad (44)$$

Since at this steady state the Jacobian of the fast system is defined as

$$J_{xy}^a = \begin{pmatrix} -\hat{x}_a\left(r + \hat{E}'(\hat{x}_a)\right) & -\hat{x}_aQ(d, \gamma) \\ \hat{y}_aQ(d, \gamma) & 0 \end{pmatrix} \quad (45)$$

it follows that if the policy function has a positive slope, $\hat{E}'(\hat{x}_a) > 0$, then the slow manifold is attracting by an argument similar to that in Result 1.[12]

On the slow manifold mutation dynamics are given by

$$\dot{d} = -\mu_d\hat{x}_a\hat{y}_a\frac{\partial Q(d, \gamma)}{\partial d} \quad (46)$$

$$\dot{\gamma} = \mu_\gamma\hat{x}_a\hat{y}_a\frac{\partial Q(d, \gamma)}{\partial \gamma} \quad (47)$$

and the existence, or not, of Red Queen cycles is governed by result 1.

Assume that trait dynamics converge to a point attractor (d^*, γ^*), then the host - parasite biomasses and the policy function will converge to

$$x_a^* = \hat{x}_a(d^*, \gamma^*), \ y_a^* = \hat{y}_a(d^*, \gamma^*), \ E_a^* = \hat{E}(x_a^*)$$

Then from (33) the steady state valuation of the system with convergence in

---

[12] Although at this level of generality it is not possible to determine the slope of the policy function, intuitively it is expected to have a positive slope. Effort increases at higher biomass levels.

slow time will be

$$V^* = \frac{S\left(qE_a^* x_a^*\right) - cE_a^*}{\rho} \tag{48}$$

On the other hand the perceived valuation of the system with convergence in fast time and when parasite dynamics and trait dynamics are ignored is

$$\hat{V}_f = \frac{S\left(q\hat{E}_f x_f^*\right) - c\hat{E}_f}{\rho} \tag{49}$$

It is clear that the difference

$$V^* - \hat{V}_f$$

will provide a measure of the change in the valuation of the system when parasite dynamics and trait dynamics are ignored.

2.3.2 Optimal harvesting rules in fast time scale[13]

The problem is to maximize (31) subject to (1), (2) for fixed ("frozen") values of d and γ. When the traits take their initial values (d_0, γ_0), the solution corresponds to the boundary layer problem. The dynamic programming equation becomes for the fast system:

$$\rho V^0\left(x, y\right) = \max_E \mathcal{H}^0\left(x, y, \frac{\partial V}{\partial x}, \frac{\partial V}{\partial y}\right)$$

$$\mathcal{H}^0 = \max_E \left\{ S\left(qEx\right) - cE + p_x\left(x\left(s - rx - yQ\left(\bar{d}, \bar{\gamma}\right)\right) - qEx\right) \right.$$

$$\left. + p_y\left(xQ\left(\bar{d}, \bar{\gamma}\right) - \delta\right) \right\} \quad p_x = \frac{\partial V^0}{\partial x}, \ p_y = \frac{\partial V^0}{\partial y}$$

Let $E^0 = E^0\left(x, y; d_0, \gamma_0\right) = E^0\left(x, y\right)$ be the relevant policy function which at the fast time steady state $\left(x_f^0, y_f^0\right)$, assuming that it exists, will be $E_f^0 = E^0\left(x_f^0, y_f^0; d_0, \gamma_0\right)$. Then the perceived steady state valuation of the system in fast time will be

$$V_f^0 = \frac{S\left(qE_f^0 x_f^0\right) - cE_f^0}{\rho}$$

---

[13]In the terminology of singular perturbation analysis, the solution to this control problem results in the *fast controller*.

At the fast time steady state, the equilibrium values for x and y, assuming positive abundance in equilibrium and stability, will be

$$x_f^0 = x_f^0(d_0, \gamma_0) = \frac{\delta}{Q(d_0, \gamma_0)} \ , \ y_f^0 = y_f^0(d_0, \gamma_0) = \frac{s - r\hat{x} - qE_f^0\left(x_f^0, y_f^0; d_0, \gamma_0\right)}{Q(d_0, \gamma_0)}$$
(50)

Then mutation dynamics are given by

$$\dot{d} = -\mu_d x_f^0 y_f^0 \frac{\partial Q(d, \gamma)}{\partial d} \tag{51}$$

$$\dot{\gamma} = \mu_\gamma x_f^0 y_f^0 \frac{\partial Q(d, \gamma)}{\partial \gamma} \tag{52}$$

and the existence of Red Queen cycles is governed by result 2.

Assume as before that trait dynamics converge to a point attractor (d^*, γ^*), then the host - parasite biomasses and the policy function will converge to

$$x^{0*} = x_f^0(d^*, \gamma^*), \ y^{0*} = y_f^0(d^*, \gamma^*), \ E^{0*} = E_f^0(x^*, y^*, d^*, \gamma^*)$$

Then from (36) the steady state valuation of the system with convergence in slow time will be

$$V^{0*} = \frac{S\left(qE^{0*}x^{0*}\right) - cE^{0*}}{\rho} \tag{53}$$

The difference

$$V^{0*} - V_f^0$$

will provide a measure of the change in the valuation of the system when only a fast controller is designed, and slow trait dynamics are not taken into account.

2.3.3 The SOMP

To analyze the SOMP we consider the optimal control problem of maximizing (31) subject to the constraints of the slow dynamics (9), (10) which evolve on the slow manifold (11).[14]

---

[14]This is the *slow controller*. See, for example, Pan and Başar (1996).

The current value Hamiltonian for this problem is

$$
\mathcal{H}^S = S(qE\hat{x}) - cE + \lambda \left[-\mu_d \hat{x}\hat{y} \frac{\partial Q(d,\gamma)}{\partial d} \right] + \zeta \left[\mu_\gamma \hat{x}\hat{y} \frac{\partial Q(d,\gamma)}{\partial \gamma} \right], (54)
$$

$$
\hat{x} = \frac{\delta}{Q(d,\gamma)}, \hat{y} = \frac{s - r\hat{x} - qE}{Q(d,\gamma)}
$$

By **Result 1** the steady state $(\hat{x}, \hat{y}) > 0$ is asymtotically stable, therefore the optimal control problem is solved on the attracting part of the slow manifold.

The maximum principle implies that optimal effort is chosen as:

$$
S'\left(qE\frac{\delta}{Q(d,\gamma)} \right) \frac{q\delta}{Q(d,\gamma)} - c + \tag{55}
$$

$$
\left(\lambda\mu_d - \zeta\mu_\gamma \right) \frac{q\delta}{[Q(d,\gamma)]^2} \frac{\partial Q(d,\gamma)}{\partial d} = 0 \tag{56}
$$

$$
\text{or } \tilde{E}_s = \tilde{E}_s(d,\gamma,\lambda,\zeta)
$$

By comparing (55) with (37) it is interesting to note that in the POMP marginal effort benefits net of effort costs are adjusted by the shadow value of the resource's biomass p_x, which is the standard approach in resource economics. In contrast in the SOMP the adjustment is related to the shadow values of the traits and the impact of mutation on fitness. This implies that if mutation is taken into account, regulation should be adjusted appropriately.

The Modified Hamiltonian Dynamic System in this case becomes

$$
\dot{\lambda} = \rho\lambda - \frac{\partial \mathcal{H}}{\partial d} \tag{57}
$$

$$
\dot{\zeta} = \rho\zeta - \frac{\partial \mathcal{H}}{\partial \gamma} \tag{58}
$$

$$
\dot{d} = \frac{\partial \mathcal{H}}{\partial \lambda} = -\mu_d \hat{x}\hat{y} \frac{\partial Q(d,\gamma)}{\partial d} \tag{59}
$$

$$
\dot{\gamma} = \frac{\partial \mathcal{H}}{\partial \zeta} = \mu_\gamma \hat{x}\hat{y} \frac{\partial Q(d,\gamma)}{\partial \gamma} \tag{60}
$$

along with (9), (10), with everything evaluated at $\hat{x}, \hat{y}, \tilde{E}_s = \tilde{E}_s(d,\gamma,\lambda,\zeta)$.

Assume that a steady state $(d^*, \gamma^*, \lambda^*, \zeta^*)$ for the system (57) - (60) exists

and consider the curvature matrix:

$$Q\left(d,\gamma,\lambda,\zeta\right) = \begin{pmatrix} \frac{\partial^2 \mathcal{H}}{\partial d^2} & \frac{\partial^2 \mathcal{H}}{\partial d \partial \gamma} & \frac{-\rho}{2} & 0 \\ \frac{\partial^2 \mathcal{H}}{\partial d \partial \gamma} & \frac{\partial^2 \mathcal{H}}{\partial \gamma^2} & 0 & \frac{-\rho}{2} \\ \frac{-\rho}{2} & 0 & -\frac{\partial^2 \mathcal{H}}{\partial \lambda^2} & -\frac{\partial^2 \mathcal{H}}{\partial \lambda \partial \zeta} \\ 0 & \frac{-\rho}{2} & -\frac{\partial^2 \mathcal{H}}{\partial \lambda \partial \zeta} & -\frac{\partial^2 \mathcal{H}}{\partial \zeta^2} \end{pmatrix}$$

Result 2: *If the curvature matrix $Q\left(d^*,\gamma^*,\lambda^*,\zeta^*\right)$ is negative definite, then by the Brock and Sheinkman (1976) condition all solutions of (57) - (60) which are bounded for $t \geq 0$ converge to $(d^*,\gamma^*,\lambda^*,\zeta^*)$ as $t \to \infty$.*

If the conditions of Result 2 prevail, then Red Queen dynamics are removed by optimal management.

Assume that the policy function for this problem is given by

$$\bar{E} = \bar{E}\left(d,\gamma\right)$$

with $\bar{E}^* = \bar{E}\left(d^*,\gamma^*\right)$ at the optimal steady state. Then the socially-optimal steady state valuation would be

$$
\begin{aligned}
V^{S*} &= \frac{S\left(q\bar{E}^*\bar{x}^*\right) - c\bar{E}^*}{\rho} \\
\bar{x}^* &= \frac{\delta}{Q\left(d^*,\gamma^*\right)} \; , \; \bar{y}^* = \frac{s - r\bar{x}^* - q\bar{E}^*}{Q\left(d^*,\gamma^*\right)}
\end{aligned}
\tag{61}
$$

The optimal steady state valuation (61) can be augmented by allowing for an additional value which is associated with the host biomass (e.g. existence value). In this case the flow of benefits would be $S\left(qEc\right) - cE + B\left(x\right)$, where $B\left(x\right)$ is an increasing concave function reflecting existence values. The optimal steady state valuation becomes

$$V_1^{S*} = \frac{S\left(q\bar{E}^*\bar{x}^*\right) - c\bar{E}^* + B\left(\bar{x}^*\right)}{\rho} \tag{62}$$

It is clear that the differences

$$V_1^{S*} - V^{0*} \quad \text{or} \quad V_1^{S*} - V^* \tag{63}$$

reflect the difference between the socially-optimal valuation of the system and the valuation of the system when trait dynamics and parasite dynamics are ignored. This measure can be regarded as a measure of the costs from deviating from socially-optimal management.

3 A general coevolutionary model with many hosts and parasites

Having seen how to model harvesting decisions in a system with one host and one parasite, we move now to a more general case. Combining Krakauer and Jansen's (2002) generalization to two hosts and two parasites, and allowing interspecies interactions, a model with many hosts and parasites could be developed. In this section, and in order to keep things as simple as possible, we develop a two-host, two-parasite model, with the host species interacting in the context of a mutualism model (Murray 2003).[15] The structure of the model for the host parasite part, where the host is "useful" in the sense of being harvested at harvest rates $h_i = q_i E_i x_i, i = 1, 2$ respectively, with both host and parasite evolving in fast time, is:[16]

$$\varepsilon \dot{x}_1 = x_1 \left(s_1 - r_1 x_1 - a_{12} x_2 - y_1 Q\left(d_1, \gamma_1\right) - y_2 Q\left(d_1, \gamma_2\right)\right) - h_1 \quad (64)$$

$$\varepsilon \dot{x}_2 = x_2 \left(s_2 - r_2 x_2 - a_{21} x_1 - y_1 Q\left(d_2, \gamma_1\right) - y_2 Q\left(d_2, \gamma_2\right)\right) - h_2 \quad (65)$$

$$\varepsilon \dot{y}_1 = y_1 \left(x_1 Q\left(d_1, \gamma_1\right) + x_2 Q\left(d_2, \gamma_1\right) - \delta\right) \quad (66)$$

$$\varepsilon \dot{y}_2 = y_2 \left(x_1 Q\left(d_1, \gamma_2\right) + x_2 Q\left(d_2, \gamma_2\right) - \delta\right) \quad (67)$$

The flow of benefits from each useful species, assuming separable benefits in each species harvesting to simplify things, is given by

$$\sum_{i=1}^{2} \left[S\left(q_i E_i x_i\right) - c_i E_i + B_i\left(x_i\right)\right]$$

---

[15]The generalization to any number of species and parasites is straightforward.

[16]In terms of our previous notation, $h_i = q_i E_i x_i, i = 1, 2$.

where $B_i(x_i)$ is a monotonically increasing and strictly concave function that reflects benefits associated with the biomass of each species (e.g. existence values). If no existence values are imputed then $B_i(x_i)$ is identically zero.

If we consider the 'myopic' benefit maximization problem where parasite dynamics and slow mutation is ignored, the problem becomes

$$\max_{\{E_1(t),E_1(t)\}} \int_0^\infty e^{-\rho t} \left[\sum_{i=1}^2 [S(q_i E_i x_i) - c_i E_i + B_i(x_i)] \right] dt \qquad (68)$$

$$s.t. \frac{dx_1}{d\tau} = x_1(s_1 - r_1 x_1 - a_{12} x_2 - Y_1) - h_1 \qquad (69)$$

$$\frac{dx_2}{d\tau} = x_2(s_2 - r_2 x_2 - a_{21} x_2 - Y_2) - h_2 \qquad (70)$$

$$Y_1 = y_1 Q(d_1, \gamma_1) + y_2 Q(d_1, \gamma_2) \text{ fixed} \qquad (71)$$

$$Y_2 = y_1 Q(d_1, \gamma_1) - y_2 Q(d_1, \gamma_2), \ i = 1, 2 \qquad (72)$$

where Y_i represents parasite and mutation effects which are treated as fixed parameters in the 'myopic' model.

Let the dynamic programming equation be

$$\rho V(x_1, x_2) = \max_{E_1, E_2} \left\{ \sum_{i=1}^2 [S(q_i E_i x_i) - c_i E_i + B_i(x_i)] + \frac{\partial V}{\partial x_1} \frac{dx_1}{d\tau} + \frac{\partial V}{\partial x_2} \frac{dx_2}{d\tau} \right\}$$

and let $\hat{E}_i = \hat{E}_i(x_1, x_2)$ be the policy function associated with the problem.

To analyze the impact of the "myopic" behavior on the whole system, we consider the slow manifold consisting of the equilibria of the boundary layer problem. For $\mathbf{d} = (d_1, d_2)$, $\boldsymbol{\gamma} = (\gamma_1, \gamma_2)$ the slow manifold can be locally parametrized by $\mathbf{x} = (x_1, x_2)$, $\mathbf{y} = (y_1, y_2)$ as

$$M = \left\{ \begin{array}{l} (\mathbf{x}, \mathbf{y}; \mathbf{d}, \boldsymbol{\gamma}): x_1(s_1 - r_1 x_1 - a_{12} x_2 - y_1 Q(d_1, \gamma_1) - y_2 Q(d_1, \gamma_2)) \\ \qquad\qquad - q_1 \hat{E}_1(x_1, x_2) x_1 = 0, \\ x_2(s_2 - r_2 x_2 - a_{21} x_1 - y_1 Q(d_2, \gamma_1) - y_2 Q(d_2, \gamma_2)) \\ \qquad\qquad - q_2 \hat{E}_2(x_1, x_2) x_2 = 0, \\ y_1(x_1 Q(d_1, \gamma_1) + x_2 Q(d_2, \gamma_1) - \delta) = 0, \\ y_2(x_1 Q(d_1, \gamma_2) + x_2 Q(d_2, \gamma_2) - \delta) = 0 \} \end{array} \right. \qquad (73)$$

Equilibrium abundances for the fast host-parasite system are then defined as

$$\tilde{x}_i = \tilde{x}_i\left(\mathbf{d}, \boldsymbol{\gamma}\right), \ \tilde{y}_i = \tilde{y}_i\left(\mathbf{d}, \boldsymbol{\gamma}\right), i = 1, 2 \tag{74}$$

The stability of the equilibria for the boundary layer problem and thus the attracting parts of the slow manifold depend on the linearization matrix

$$J_2 = \begin{pmatrix} -x_1\left(r_1 + q_1 \frac{\partial \hat{E}_1}{\partial x_1}\right) & -x_1\left(a_{12} + q_1 \frac{\partial \hat{E}_1}{\partial x_2}\right) & -x_1 Q_{11} & -x_1 Q_{12} \\ -x_2\left(a_{21} + q_2 \frac{\partial \hat{E}_2}{\partial x_1}\right) & -x_2\left(r_2 + q_2 \frac{\partial \hat{E}_2}{\partial x_2}\right) & -x_2 Q_{21} & -x_2 Q_{22} \\ y_1 Q_{11} & y_1 Q_{12} & 0 & 0 \\ y_2 Q_{21} & y_2 Q_{22} & 0 & 0 \end{pmatrix} \tag{75}$$

where $Q_{ij} = Q\left(d_i, \gamma_j\right), i, j = 1, 2$. The trace of J_2 is defined as:

$$tr J_2 = -x_1\left(r_1 + q_1 \frac{\partial \hat{E}_1}{\partial x_1}\right) - x_2\left(r_2 + q_2 \frac{\partial \hat{E}_2}{\partial x_2}\right) \lesseqqgtr 0$$

and its sign depends on the parameters of the problem and the slope of the policy function. On the other hand, $\det J_2 = x_1 x_2 y_1 y_2 \left(Q_{11}Q_{22} - Q_{12}Q_{21}\right)^2 \geq 0$. Therefore, the slow manifold might have attracting and non attracting parts.

Then, mutation evolving in slow time implies, for the stable equilibria of the population dynamics problem,

$$\begin{aligned} \dot{d}_1 &= -\mu_d \tilde{x}_1 \left(\tilde{y}_1 \left. \frac{\partial Q\left(d, \gamma_1\right)}{\partial d} \right|_{d=d_1} + \tilde{y}_2 \left. \frac{\partial Q\left(d, \gamma_2\right)}{\partial d} \right|_{d=d_1} \right) \\ \dot{d}_2 &= -\mu_d \tilde{x}_2 \left(\tilde{y}_1 \left. \frac{\partial Q\left(d, \gamma_1\right)}{\partial d} \right|_{d=d_2} + \tilde{y}_2 \left. \frac{\partial Q\left(d, \gamma_2\right)}{\partial d} \right|_{d=d_2} \right) \\ \dot{\gamma}_1 &= \mu_\gamma \tilde{y}_1 \left(\tilde{x}_1 \left. \frac{\partial Q\left(d_1, \gamma\right)}{\partial d} \right|_{\gamma=\gamma_1} + \tilde{x}_2 \left. \frac{\partial Q\left(d_2, \gamma\right)}{\partial d} \right|_{\gamma=\gamma_1} \right) \\ \dot{\gamma}_2 &= \mu_\gamma \tilde{y}_2 \left(\tilde{x}_1 \left. \frac{\partial Q\left(d_1, \gamma\right)}{\partial d} \right|_{\gamma=\gamma_2} + \tilde{x}_2 \left. \frac{\partial Q\left(d_2, \gamma\right)}{\partial d} \right|_{\gamma=\gamma_2} \right) \end{aligned} \tag{76}$$

If a point attractor $\left(\mathbf{d}^*, \boldsymbol{\gamma}^*\right)$ exists for $\left(\mathbf{d}, \boldsymbol{\gamma}\right)$, then the steady states for the

host parasite system and the steady state harvesting are defined as:

$$\tilde{x}_i^* = \tilde{x}_i\left(\mathbf{d}^*, \boldsymbol{\gamma}^*\right), \tilde{y}_i^* = \tilde{y}_i\left(\mathbf{d}^*, \boldsymbol{\gamma}^*\right) \ , \tilde{E}_i^* = \tilde{E}_i\left(x_1^*, x_2^*\right), \ i = 1, 2 \qquad (77)$$

In this case the steady state valuation of the system is:

$$V^* = \frac{\sum_{i=1}^2 \left[S\left(q_i^* \tilde{E}_i^* \tilde{x}_i^*\right) - c_i^* \tilde{E}_i^* + B_i\left(\tilde{x}_i^*\right)\right]}{\rho}$$

It should be noticed that the modeling is fairly general and allows for jumps in the population variables, if the boundary layer problem is close to a non attracting part of the slow manifold M. In this case noise might cause the population variable to jump and move very fast to another part of M.

Consider now the SOMP problem where (68) is maximized subject to the trait dynamics on an attractive part of the slow manifold. The problem is formally defined as

$$\max_{\{E_1(t), E_1(t)\}} \int_0^\infty e^{-\rho t} \left[\sum_{i=1}^2 \left[S\left(q_i E_i x_i\right) - c_i E_i + B_i\left(x_i\right)\right]\right] dt$$

subject to:

$$\dot{d}_1 = -\mu_d \hat{x}_1 \left(\hat{y}_1 \left.\frac{\partial Q\left(d, \gamma_1\right)}{\partial d}\right|_{d=d_1} + \hat{y}_2 \left.\frac{\partial Q\left(d, \gamma_2\right)}{\partial d}\right|_{d=d_1}\right)$$

$$\dot{d}_2 = -\mu_d \hat{x}_2 \left(\hat{y}_1 \left.\frac{\partial Q\left(d, \gamma_1\right)}{\partial d}\right|_{d=d_2} + \hat{y}_2 \left.\frac{\partial Q\left(d, \gamma_2\right)}{\partial d}\right|_{d=d_2}\right)$$

$$\dot{\gamma}_1 = \mu_\gamma \hat{y}_1 \left(\hat{x}_1 \left.\frac{\partial Q\left(d_1, \gamma\right)}{\partial d}\right|_{\gamma=\gamma_1} + \hat{x}_2 \left.\frac{\partial Q\left(d_2, \gamma\right)}{\partial d}\right|_{\gamma=\gamma_1}\right)$$

$$\dot{\gamma}_2 = \mu_\gamma \hat{y}_2 \left(\hat{x}_1 \left.\frac{\partial Q\left(d_1, \gamma\right)}{\partial d}\right|_{\gamma=\gamma_2} + \hat{x}_2 \left.\frac{\partial Q\left(d_2, \gamma\right)}{\partial d}\right|_{\gamma=\gamma_2}\right) \qquad (78)$$

where $\hat{\mathbf{x}} = \hat{\mathbf{x}}\left(\mathbf{d}, \boldsymbol{\gamma}, \mathbf{E}\right), \hat{\mathbf{y}} = \hat{\mathbf{y}}\left(\mathbf{d}, \boldsymbol{\gamma}, \mathbf{E}\right)$ are defined by the solutions of the al-

gebraic equations on the slow manifold

$$
\hat{M} = \begin{cases} (\mathbf{x}, \mathbf{y}; \mathbf{d}, \boldsymbol{\gamma}) : x_1 \left(s_1 - r_1 x_1 - a_{12} x_2 - y_1 Q \left(d_1, \gamma_1 \right) - y_2 Q \left(d_1, \gamma_2 \right) \right) \\ \qquad\qquad\qquad - q_1 E_1 x_1 = 0, \end{cases}
$$
$$
\begin{aligned}
x_2 \left(s_2 - r_2 x_2 - a_{21} x_1 - y_1 Q \left(d_2, \gamma_1 \right) - y_2 Q \left(d_2, \gamma_2 \right) \right) & \\
- q_2 E_2 x_2 = 0, & \\
y_1 \left(x_1 Q \left(d_1, \gamma_1 \right) + x_2 Q \left(d_2, \gamma_1 \right) - \delta \right) = 0, & \qquad (79) \\
y_2 \left(x_1 Q \left(d_1, \gamma_2 \right) + x_2 Q \left(d_2, \gamma_2 \right) - \delta \right) = 0 \}
\end{aligned}
$$

The dynamic programming equation for this problem is

$$
\rho V^S = \max_{E_1, E_2} \left\{ \sum_{i=1}^{2} \left[S \left(q_i E_i x_i \right) - c_i E_i + B_i \left(x_i \right) \right] + \partial \mathbf{V}_{\mathbf{d}}^S \dot{\mathbf{d}} + \partial \mathbf{V}_{\boldsymbol{\gamma}}^S \dot{\boldsymbol{\gamma}} \right\} \qquad (80)
$$

Then if $\hat{E}_i = \hat{E}_i \left(\mathbf{d}, \boldsymbol{\gamma} \right)$ is the policy function for this problem, and $\left(\mathbf{d}^S, \boldsymbol{\gamma}^S \right)$ is a steady state point attractor, the corresponding steady-state values for the host-parasite system and harvesting will be

$$
\hat{x}_i^S = \hat{x}_i \left(\mathbf{d}^S, \boldsymbol{\gamma}^S \right), \; \hat{y}_i^S = \hat{y}_i \left(\mathbf{d}^S, \boldsymbol{\gamma}^S \right), \; \hat{E}_i^S = \hat{E}_i \left(\hat{x}_1^S, \hat{x}_2^S \right), \; i = 1, 2 \qquad (81)
$$

By comparing (77) with (81) we can determine the changes in the ecosystems diversity as expressed by the abundances in $\mathbf{x}, \mathbf{y}$ as well tas he deviations between the steady state privately optimal and socially optimal harvesting rules. Since the steady-state valuation of the socially-optimal system is

$$
V^S = \frac{\sum_{i=1}^{2} \left[S \left(q_i \hat{E}_i^S \hat{x}_i^S \right) - c_i^* \hat{E}_i^S + B_i \left(\hat{x}_i^S \right) \right]}{\rho}
$$

the difference $V^S - V^*$ denotes the change in the system value from not taking into account the antagonistic coevolution of species and pests or parasites in the system when we design the harvesting rule. To put it differently, the difference reflects the change in steady-state valuation by ignoring the Red Queen dynamics in our harvesting rule.

Since V^S and V^* represent the ecosystems valuations corresponding to

different biodiversity patterns, the difference $V^S - V^*$ can also be used to value changes in biodiversity. This result in a sense complements and extends the result of Brock and Xepapadeas (2004) about biodiversity valuation through the Bellman state valuation function, to the multi-species case with antagonistic coevolution.

4   Ecosystem Sustainability Criteria

The most commonly used definition of sustainable development now is that of the Brundtland Report stating that:

> "[Sustainable development is] development which meets the needs
> of the present without compromising the ability of future gener-
> ations to meet their own needs".

The concept of sustainable development is at the center of current concerns about environment and development. It is not only the best known and most commonly cited idea linking environment and development, it is also the best worked-out, in that it is the capstone of the World Conservation Strategy.

In the attempt to make the definition of sustainability operational and useful for the development of sustainability criteria and the design of sustainable policies, many auxiliary definitions have been developed. A more recent and prevailing one is a definition associated with non declining well being.

The idea of non declining well being was formulated by Dasgupta and Mäler (2001) in order to define sustainability as *the non declining genuine wealth*. The idea is that each generation should bequeath to each successor at least as large a *productive base* as it inherited from its predecessors. For this to be achieved, the productive base of the economy should be preserved for the next generations. The productive base includes a list of assets: *Manufactured capital, human capital, natural capital and knowledge. Genuine investment* is the sum of the investment in the above forms of capital valued at accounting prices. If genuine investment is non-decreasing over time,

then welfare is also non-decreasing and the development is sustainable. In a similar way Pemberton and Ulph (2001), stated that:

"an economy was acting in a sustainable fashion at a particular moment of time, if the value obtained from the vector of capital stocks it was passing on to the future was the same as the value obtained from the vector of capital stocks it inherited. Alternatively, an economy was instantaneous value sustainable[17] if the instantaneous rate of change of its value at a particular moment of time, was zero".[18]

The above definitions suggests that:

Definition 1 *If the value for the economy, or equivalently, the intergenerational well being is defined as:*

$$v_t = \int_t^\infty e^{-\delta(\tau-t)} f_o\left(\mathbf{x}\left(\tau\right), \mathbf{u}\left(\tau\right)\right) d\tau, \ \delta > 0, \ \tau \geq t \tag{82}$$

$$\dot{x}_i = f_i\left(\mathbf{x}\left(\tau\right), \mathbf{u}\left(\tau\right)\right), \ i = 1, ..., n, \ x\left(0\right) = x_o, \ \textit{fixed} \tag{83}$$

$$\mathbf{x} \in A, \quad \mathbf{u} \in U$$

where $\mathbf{x}$ *and* $\mathbf{u}$ *define the state and control vector respectively and* $f_i\left(\cdot, \cdot\right)$ *are the equations of motion of the system, then, the economy is sustainable for any feasible control path* $\mathbf{u}\left(\tau\right)$ *and the associated state path* $\mathbf{x}\left(\tau\right)$ *generated by (83) if the value is not declining, or*

$$\frac{dv_t}{dt} \geq 0 \tag{84}$$

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[17]*Instantaneous value sustainability* requires that the present value of future utility be constant at an instant of time.(Pemberton and Ulph 2001).

[18]While permanent flow sustainability requires the flow of utility to be constant for all future time, instantaneous value sustainability requires that the present value of all future utility be constant at an instant of time. Associated with the concept of instantaneous value sustainability, Pemberton and Ulph define instantaneous constant value income as the maximum amount that an economy could consume at a moment of time and keep the maximum present value of all future utility constant.

The controls can be chosen optimally to maximize (82) subject to (83), or by some arbitrary feedback rule.[19] In any case we can write $\mathbf{u} = \mathbf{u}(\mathbf{x})$ and this could represent either the policy function of the optimization problem or the arbitrary feedback control rule. Then the solution of the transition equations will provide paths for the state variables depending on initial conditions or

$$\mathbf{x}(\tau) = \boldsymbol{\phi}(\mathbf{x}_t, \tau - t), \ \tau \geq t \tag{85}$$

Substituting (85) into value (82) we obtain the value of the economy as a function of the initial stocks of the state variables, which in actual applications would be different types of capital stock (e.g. man made, human, natural capital), or:

$$v_t(\mathbf{x}_t) = \int_t^\infty e^{-\delta(\tau-t)} f_o\left(\boldsymbol{\phi}(\mathbf{x}_t, \tau - t), \mathbf{u}(\boldsymbol{\phi}(\mathbf{x}_t, \tau - t))\right) d\tau \tag{86}$$

The accounting or shadow price for state variable x_i at time t is defined as

$$q_{it} = \frac{\partial v_t(\mathbf{x}_t)}{\partial \mathbf{x}_{it}} \tag{87}$$

The sustainability criterion (84) is satisfied if

$$\mathcal{S} = \frac{dv_t}{dt} = \sum_{i=1}^n q_{it} \frac{\partial x_i}{\partial t} \geq 0 \tag{88}$$

Thus sustainability requires that genuine investment, measured as the sum of rate of change in the state variables (capital stocks) valued at the corresponding accounting prices, be non declining at time t. This is a local measure which can become non local by integrating (88) (Arrow, Dasgupta and Mäler 2003).

It is clear that this type of methodology can be applied in order to explore the sustainability of ecosystems, where the value of the ecosystem or the well

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[19]For example in the classic Solow model of economic growth, the control variable consumption is chosen as a fixed proportion of output, or $c = (1-s)f(k)$, where k is capital stock which is the the state variable, and $f(k)$ is a neoclassical production function. This consumption rule is a feedback rule, not an optimizing one.

being associated with it, from the human point of view, is determined using function (68) as:

$$v_t\left(\mathbf{d}_t, \boldsymbol{\gamma}_t\right) = \int_t^\infty e^{-\rho(\tau-t)} \left[\sum_{i=1}^2 \left[S\left(q_i E_i x_i\right) - c_i E_i + B_i\left(x_i\right)\right]\right] d\tau \qquad (89)$$

subject to the relevant dynamic constraints.

It should be noticed that different approaches to ecosystem management correspond to different sustainability conditions.

Assume that the ecosystem is managed by ignoring parasite dynamics and mutation. Then the only relevant state variables, from the manager's point of view, are the populations of the useful species. The manager will use as accounting prices the costate variables associated with problem (68), $p_{x_i} = \partial V/\partial x_i$, and the sustainability criterion for the ecosystem will be

$$\mathcal{S}_m = \sum_{i=1}^2 p_{x_i} \dot{x}_i \qquad (90)$$

This is, however, the wrong measure since the harvesting effort is not chosen in a socially optimal way and parasite dynamics and mutation is ignored. The equilibrium abundances of host parasites on the slow manifold (73) and the policy functions, are determined by (74) as $\tilde{x}_i = \tilde{x}_i\left(\mathbf{d}, \boldsymbol{\gamma}\right), \tilde{y}_i = \tilde{y}_i\left(\mathbf{d}, \boldsymbol{\gamma}\right)$, $\tilde{E}_i = \tilde{E}_i\left(x_1, x_2\right)$, $i = 1, 2$. Then the solution of the system (76) will determine time paths for the state variables $\left(\mathbf{d}, \boldsymbol{\gamma}\right): \mathbf{d}_\tau = \tilde{\mathbf{d}}\left(\mathbf{d}_t, \tau - t\right)$, $\boldsymbol{\gamma}_\tau = \tilde{\boldsymbol{\gamma}}\left(\boldsymbol{\gamma}_t, \tau - t\right)$. Then the value of the ecosystem is defined as

$$\begin{aligned}
v_t\left(\mathbf{d}_t, \boldsymbol{\gamma}_t\right) &= \int_t^\infty e^{-\rho(\tau-t)} \left[\sum_{i=1}^2 \left[S\left(q_i \tilde{E}_i \tilde{x}_i\right) - c_i \tilde{E}_i + B_i\left(\tilde{x}_i\right)\right]\right] d\tau \quad (91) \\
\tilde{E}_i &= \tilde{E}_i\left(\mathbf{x}\right) = \tilde{E}_i\left(\tilde{\mathbf{x}}\left(\tilde{\mathbf{d}}\left(\mathbf{d}_t, \tau - t\right), \tilde{\boldsymbol{\gamma}}\left(\boldsymbol{\gamma}_t, \tau - t\right)\right)\right) \\
\tilde{x}_i &= \tilde{x}_i\left(\left(\tilde{\mathbf{d}}\left(\mathbf{d}_t, \tau - t\right), \tilde{\boldsymbol{\gamma}}\left(\boldsymbol{\gamma}_t, \tau - t\right)\right)\right)
\end{aligned}$$

and the local sustainability criterion for the ecosystem at time t will be

$$\mathcal{S}_a = \sum_{i=1}^{2} \left(\frac{\partial v_t}{\partial d_{it}} \dot{d}_{it} + \frac{\partial v_t}{\partial \gamma_{it}} \dot{\gamma}_{it} \right) \geq 0 \qquad (92)$$

It is interesting to note that sustainability depends on the growth of traits along a path implied by the harvesting rule and the corresponding accounting prices. The accounting price for a trait could be positive or negative indicating the impact of the trait on the value of the system. In this case it is mutation, the slow variable, that determines the sustainability conditions of the ecosystem. By comparing (90) with (92), it is clear that the perceived sustainability of the ecosystem determined by population dynamics alone through (90), might be different from the "true" sustainability conditions of the ecosystem which are determined by the slow evolution of mutation. Thus sustainability criteria based on resource biomass might produce misleading results regarding ecosystem sustainability, and are likely to require correction by taking into account the evolution of slow variables reflected in mutation.

In the social optimization model the sustainability criterion (92) remains the same with the difference that the accounting prices are determined by the system of differential equations resulting from the Pontryagin principle. That is

$$\dot{q}_{d_i} = \rho q_{d_i} - \frac{\partial \mathcal{H}^{oS}}{\partial d_i} \ , i = 1, 2 \qquad (93)$$

$$\dot{q}_{\gamma_i} = \rho q_{\gamma_i} - \frac{\partial \mathcal{H}^{oS}}{\partial \gamma_i} \ , i = 1, 2$$

where $\mathcal{H}^{oS}$ is the maximized Hamiltonian associated with the dynamic programming equation (80).

Comparison of the local sustainability criterion (92) calculated using the accounting prices resulting from the "not fully optimal model," with the criterion calculated using the optimal accounting prices (93), could reveal some insights regarding ecosystem sustainability when the full dynamics of coevolution are not taken into account by management decisions.

5 Concluding Remarks

In this paper we seek to provide a unified economic/ecological conceptual framework of ecosystem management when antagonistic coevolution among species takes place. In our model population dynamics govern species' or parasites' biomasses and evolve in fast time scale, while mutation characterizes the evolution of traits, and evolves in slow time scale.

We analyze various harvesting decision which could be suboptimal by disregarding parasite dynamics and mutation, or fully optimal by taking into account all the dynamic constraints of the problem, using the fast time scale - slow time scale formalism.

We provide sufficient conditions under which human intervention through harvesting could disrupt Red Queen cycles, and we also provide, using Bellmans state valuation function, a measure of change in the steady-state ecosystem valuation, between suboptimal and fully-optimal decisions. Our results suggest that suboptimal decisions which ignore mutation could lead to *surprises,* in the sense that the actual evolution of the ecosystem under the influence of interacting population dynamics and mutation, could be different from the one perceived when the management rules were designed. Crucial to this is that evolution moves slowly, but not that slowly, to make the dynamics of mutation irrelevant. Although this is an empirical issue, evidence from resistance development in antibiotics or genetically-modified crops suggests that at least in certain cases evolution moves fast enough. Thus when human management disregards this evolution the outcome of human management in terms of ecosystem composition might not be the expected one.

Bellmans state valuation function can also be used to provide a measure of value of changes in biodiversity as we move from one decision framework to the other, which is a generalization of the Brock Xepapadeas (2003) result in a coevolutionary set-up..

In the same context we also adopt the concept of non declining well being as a sustainability criterion for the purpose of developing criteria for the sustainability of ecosystems. Again we distinguish the sustainability criterion between optimal and suboptimal decisions and we show that management

decisions and subsequent sustainability criteria that ignore slow variables, might obscure the fact that the actual sustainability characteristics of the ecosystem, when slow mutation, is taken into account might be completely different.

The analysis in this paper provides a conceptual framework, and at this stage lacks analytical tractability due to the complexity of the models. A future research task is to further investigate the developed framework through appropriate simulation analysis using realistic parameters for population dynamics and evolution. However the conceptual framework developed in this paper, complemented by appropriate simulations, could provide useful information about: the existence or disruption of Red Queen cycles under various management assumptions; the possibility of surprises, when mutation is ignored; the valuation of changing ecosystem diversity; as well as about the derivation of the relevant accounting prices which are necessary for defining the sustainability criterion. These types of results can also form the basis for a more efficient regulation of ecosystems, through the regulation of harvesting. Further elaboration of the fast - slow time scale framework can be used to design management rules in fast and slow time scale and, furthermore, to assist in the design of regulation in fast and slow time scales.

References

[1] Arrow K. J., Dasgupta P. and K.-G. Mäler, (2003), "Evaluating Projects and Assessing Sustainable Development in Imperfect Economies", *Environmental and Resource Economics,* 26, 647-685.

[2] Barro, R. and X. Sala-i-Martin (1995), *Economic Growth* ,Mc-Graw Hill, New York.

[3] Brock, W.A. and J. Scheinkman (1976), "The Global Asymptotic Stability of Optimal Control Systems with Applications to the Theory of Economic Growth", *Journal of Economic Growth Theory*, 12, 164-90.

[4] Brock, W. and A. Xepapadeas, (2002), "Optimal Ecosystem Management when Species Compete for Limiting Resources", *Journal of Environmental Economics and Management*, 44, 189-230.

[5] Brock, W. and A. Xepapadeas, (2004), "Valuing Biodiversity from an Economic Perspective: A Unified Economic, Ecological and Genetic Approach", *The American Economic Review*, 93(5), 1597-1614

[6] Carius, H. J.; Little, T.J. and D. Ebert,(2001), "Genetic Variation in a Host-Parasite Association: Potential for Coevolution and Frequency-Dependent Selection." *Evolution*, 2001, *55*(6), pp. 1136-45.

[7] Clark, C., (1990), *Mathematical Bioeconomics: The Optimal Management Of Renewable Resources, Second Edition*, Wiley: New York.

[8] Dasgupta P., K-G. Mäler , (2001), "Wealth as a criterion for sustainable development", *mimeo Beijer International Institute of Ecological Economics*, Swedish Academy of Sciences, Stocholm.

[9] Dieckmann, U. and R. Law (1996), "The Dynamical Theory of Coevolution: A Derivation from Stochastic Ecological Processes," *Journal of Mathematical Biology*, 34, 579-612.

[10] Kawecki, T. J. (1998), "Red Queen Meets Santa Rosalia: Arms Races and the Evolution of Host Specialization in Organisms with Parasitic Lifestyles," *The American Naturalist,* 152(4), 635-51.

[11] Krakauer, D. and V. Jansen , (2002), "Red Queen Dynamics in Protein Translation," *Journal of Theoretical Biology*, 218, 97-109.

[12] Lively, C. and M. Dybdahl, (2002), "Parasite Adaptation to Locally Common Host Genotypes." *Nature, 405*, pp. 679-81.

[13] Lorby, C., Tewfik, S. and S. Touhami, (1998), "On Tykhonov's Theorem for Convergence of Solutions of Slow nad Fast Systems," *Electronic Journal of Differential Equations*, 19, 1-22.

[14] Marrow, P. Dieckmann, U. and R. Law, (1996), "Evolutionary Dynamics of Predator Praey Systems: an ecological perspective," Journal of Mathematical Biology, 34, 556-578.

[15] Murray, J., (2003), *Mathematical Biology*, Third Edition, Berlin, Springer.

[16] Pan, Z. and T. Basar, (1996), "Model Simplification and Optimal Control of Stochastic Singularly Perturbed Systems under Exponentiated Quadratic Cost," SIAM J. Control and Optimization, 34(5), 1734-1766.

[17] Pemberton M., and D. Ulph D., (2001), "Measuring Income and Measuring Sustainability", *Scandinavian. Journal. of Economics,* 103(1), 25-40.

[18] Sastry, S. (1999), *Nonlinear Systems: Analysis, Stability and Control,* Springer, New York.

[19] Van Valen, L. (1973), "A New Evolutionary Law," *Evolutionary Theory*, 1, 1-30.

[20] Wasow, W. (1965), *Asymptotic Expansions for Ordinary Differential Equations*, Dover Phoenix Editions, N.Y.