Optimal Management of an Ecosystem with Niche Construction

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Abstract

We address the problem of optimal management of an ecosystem with niche construction along ecological succession. A dynamic carrying capacity is interpreted as depicting the dynamics of habitat creation and occupation along ecological succession. The ecosystem may have three growth modes: pure compensation (concave ecosystem regeneration function), depensation (convex-concave regeneration function) and critical depensation (additionally having negative growth rates for low biomass). We analyse the optimal policies for the management of the ecosystem for the three growth modes. Accordingly, we prove the existence of Skiba points for depensation and critical depensation ecosystems.

Keywords: Ecosystem management, ecological succession, niche creation, optimal policies, Skiba point.

JEL Classification: Q20, C61, C62

1. Introduction

We are concerned with the sustainability of ecosystems along ecological succession. Ecological succession is most simply defined as species change over time (Walker and Moral, 2003). Effective manipulations of our environment to improve fertility, productivity or diversity and an ability to mitigate undesirable conditions all depend on our ability to understand ecological succession. Humans by cropping and harvesting on ecosystems have, for long time, coped with ecological succession. They consciously manipulated the landscape to expand or improve croplands by clearing forests, draining wetlands, and flooding or burning pastures (Walker and Moral, 2003). These activities implied an intuitive awareness of ecological succession.

Historically, before 1850, most succession writings focused on practical land management issues (Walker and Moral, 2003). Subsequent observations began also to describe natural phenomena, such as succession of farms to forests. A century later, succession remains one of the most important themes in ecology (Walker and Moral, 2003). However, successional theory has still not been widely incorporated in resource management and policy design.

Another related, and widely disregarded, process in ecosystem management is niche construction (Odling-Smee et al., 2003) or bioengineering (Jones and Lawton, 1995). This idea stems from the capacity of niche-constructing organisms to modify not only their own environment but also the environments of

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other organisms in the context of shared ecosystems (Odling-Smee et al., 2003). All living creatures through their metabolism, their activities and their choices, part create and partly destroy their own niches, on scales ranging from extremely local to the global (Odling-Smee et al., 2003). Niche construction is a potent dynamic agent because in introduces biotic-abiotic-biotic feedbacks into the ecosystem dynamics besides the usual direct biotic-biotic feedbacks. For instance, most plants modify their immediate environment in some way that can impact establishment and growth of both other species and other individuals of the same species. Niche construction may effectively promote niche construction in other species (Odling-Smee et al., 2003). While these feedbacks are a common feature of ecological population models (competitive models), they are not common characteristics of ecosystem models, especially for policy design purposes.

It is interesting, in the history of ecosystem management, that the seemingly innocent observation that the activities of organisms bring about changes in the environments is so obvious, and has been familiar for science for so long, that it seems an unlikely focus for a new line of thinking (Odling-Smee et al., 2003; Walker and Moral, 2003; Jones and Lawton, 1995).

Here, we have chosen to work at the ecosystem level of organization to capture aggregate effects of ecological succession and bioengineering. In particular we are interested in using a formalism for ecological models that is suitable for policy design and analysis. The policy mechanisms that control ecosystems' production are often coarse and broad in scope – do we cut down a thousand hectares of forest, drain a thousand hectares of wetland, harvest 500,000 tons of fish? For that matter, Roughgarden (1997) argues that the policy mechanism is rarely spatially explicit or focused on individual species because of the infeasibility and cost of implementing detailed policies.

For ecosystem management, the ecosystem production function is the most useful feature of an ecological model. The ecosystem production function or ecological productivity is simply the graph of dN/dt versus N, being N the ecosystem biomass. It is a highly aggregated representation of an ecosystem's dynamics that depends on innumerable biological and spatial details (Roughgarden, 1997). We argue that ecosystem production functions should describe the biotic-abiotic-biotic feedbacks of niche construction during ecological succession.

Ecosystem models have been, for long, devised for resource (mostly fishery and forestry models) management purposes (Clark, 1976). However, they do not integrate succession theory or, niche construction feedbacks. In order to derive optimal policies along ecological succession we devise a model of an extractive economy using an ecosystem production function with niche construction along ecological succession (Mota el al., 2004). Incorporating biotic-abiotic-biotic feedbacks in the ecosystem production function leads to different growth modes for the ecosystem, and hence different optimal policies.

Depending on the parameter sets considered we may have a concave or convex-concave ecosystem production function. The kinds of behavior of optimal policies in the presence of convex-concave

ecological regeneration functions have also been seen for lake management problems (e.g., Brock and Starrett, 2003; Mäler et al. 2003), for fishing models (Dasgupta and Mäler, 2003), or for multi-species models (Scholes, 2003; Crépin, 2003) and have its bases on Skiba's (1978) work. Here we have somewhat similar results applied to the problem of managing an ecosystem along ecological succession, specially the presence of Skiba points.

2. Ecosystem dynamics revisited

In this section we briefly present the main behaviours of an ecosystem with niche construction along ecological succession. The following results and figures have been derived in Mota et al. (2004).

The dynamics of ecological succession is interpreted in terms of ecosystem biomass dynamics. Odum (1969) notes that ecological succession drives ecosystems' biomass along a logistic curve and net production along a U-inverted curve. Following this, we assume that the regeneration function for biomass is given by the logistic curve,

$$\frac{dN}{dt} = rN(CC - N) = f(N, CC),$$ (1)

where N is ecosystem biomass, CC is the ecosystem carrying capacity and r is a positive constant. This functional form is not the most common form of the logistic but it is more convenient for our purposes.

The important feature of ecological succession depicted by the logistic function is the existence of a "reasonably directional development, which culminates in a stabilized ecosystem climax" (Odum, 1969). Through ecological succession, ecosystems are driven to a climax state, representing a stable state of its structure and functioning. Ecosystem carrying capacity is the value of biomass attained at this state, established by the surrounding environment. Generally, in successional theory, these holistic principles include, if not a climax, at least a steady state between the vegetation and the environment (Walker and Moral, 2003).

However, as Walker and Moral (2003) argue, 'the more common held view now is that succession is a process of change that is not always linear and rarely reaches equilibrium'. Disturbance often redirects successional trajectories, leading to the observation that stable endpoints are rarely achieved. Actually, this idea has been appreciated for over a century and led Cowles (1901) to suggest that succession was a 'variable approaching a variable rather than a constant' (Walker and Moral, 2003). So, the obvious way to formally introduce Cowles' idea is to use a variable ecosystem carrying.

Ecosystem carrying capacity CC accounts for properties of the surrounding environment. The basic feedback introduced here to ecosystem dynamics follows from the observation that environmental change modifies ecosystem biomass dynamics (Endler, 1986), while organisms are a know source of environmental change in ecology (Jones et al. 1997). The first link is accounted by assuming that the regeneration rate of

ecosystem biomass is dependent on carrying capacity, as proposed by P. F. Verhulst in 1838. The rate of biomass accumulation is governed by factors such as, temperature, moisture, grazing, and nutrient levels as well as the type of ecosystem (Walker and Moral, 2003).

The second link has to do with ecosystem engineering and niche construction. Niche construction occurs whenever a population O changes its relativistic niche by changing a factor in its environment relative to its own features. Niche construction also occurs when a population O_1 changes the relativistic niche of a second population O_2 by changing a factor in O_2's niche. In this case it can happen that the consequences of a changed factor in O_2 niche feed forward other populations in O_1 ecosystem (Odling-smee et al., 2003). For instance, most plants modify their immediate environment in some way that can impact establishment and growth of both other species and other individuals of the same species. These include N fixation, mineral weathering by exudates, maintenance of soil organisms, influences on atmospheric deposition and impacts on the physical properties of soils (Walker and Moral, 2003).

In a successional context, Clements (1928) have identified several processes that drive succession (Walker and Moral, 2003). Clements defined reaction as the process of how plants and animals change the environment they live in. The successional consequence of reaction is facilitation, which is broadly defined as any positive interaction of one species on another, on another stage (Walker and Moral, 2003). At the community level facilitation is generally indirect. Resources may be augmented in ways that favor any nearby individuals or later arrivals through improvement of nutrient availability, substrate stability, microclimate or other variables (Walker and Moral, 2003).

This is clearly the case of ecosystem carrying capacity dependent on the ecosystem biomass' dynamics. In particular, we assume, based on a model devised by Cohen (1995) for human population dynamics, that the rate of change of ecosystem carrying capacity is proportional to the ecosystem biomass rate of change. Lewontin (1983) goes further and argues that 'organisms do not adapt to their environments; they construct them out of bits and pieces of the external world' (Odling-Smee et al., 2003). In the context of evolutionary theory, Lewontin argued that what actually happens in nature is better represented by a situation in which niche-constructing organisms and their environments are coevolving.

Along ecological succession biomass must increase for a substantial period, but eventually the mature community ceases to accumulate biomass, although the store of organic matter in the soil and in standing dead material may increase. Facilitation is most obvious during early succession when relative growth rates are high whereas in later succession may have less substantial implications (Walker and Moral, 2003). As ecosystem biomass grows, more and more individuals share benefits from niche construction. We, thus, assume that there is a diminishing rate of ecosystem productivity as biomass grows.

Accordingly, a functional form that captures these effects is :

$$\frac{dCC}{dt} = \frac{l}{N+h}\frac{dN}{dt},$$
(2)

This way the ecosystem has autocatalytic behavior, and the usual assumption ecologists make (Odling-Smee, 2003) that the environment's capacity to supply organisms with resources does not depend on the capacity of those organisms to modify their environments is now false.

The parameter l is the bioengineering capability of the ecosystem and h is the feedback saturation, since it imposes an upper limit to the intensity of biotic-abiotic-biotic feedbacks (Mota et al., 2004). Moreover, if l is high, it means that biomass has strong feedbacks with carrying capacity and small changes in population may have large effects on niche availability. This way, we are endowing the ecosystem with autocatalytic behaviour, since a rise in ecosystem biomass inflicts a rise in ecosystem carrying capacity, which creates a greater potential for biomass to grow (provided that $N < CC$).

Assuming that the dynamics of the ecosystem is governed by (1) and (2), this implies, by a change of variables, the following ecosystem production function (Mota et al., 2004):

$$\frac{dN}{dt} = rN\left(CC_l + l\ln\left(\frac{N+h}{b}\right) - N \right) \equiv R(N).$$

(3)

A simple conclusion drawn from the analogy with the logistic model is that this ecosystem has a carrying capacity given by $CC_l + l\ln\left((N+h)/b\right)$ which is constant for $l = 0$. That is, for zero bioengineering capability, we have the conventional one-population dynamics. This way, the optimum operating point of the ecosystem is not imposed on the system by exogenous conditions but depends on the historical information "remembered" by the system. Feedbacks on carrying capacity may be positive or negative depending on the ecosystem biomass for a fixed l and h.
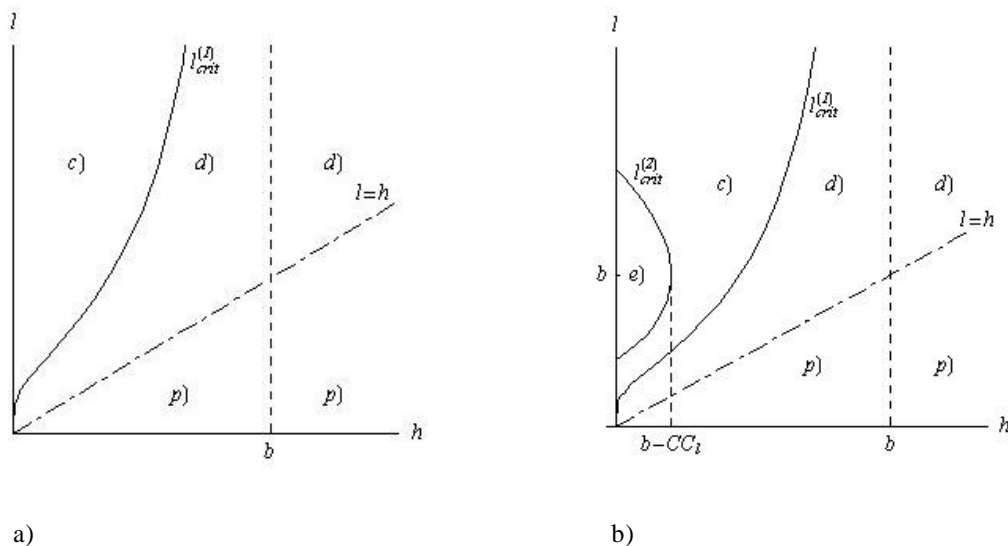

a)   b)

Figure 3.1 – a) Bifurcation diagram for the ecosystem dynamics for the case where $CC_l \geq b$. *p)* represents pure compensation; *d)* non-critical depensation and *c)* critical depensation. The line $h = b$ is the asymptote of l_{crit}^1 .

b) Bifurcation diagram for the case where $b > CC_l$. *e)* represents unconditional extinction (Mota et al., 2004).

Depending on the feedbacks on carrying capacity, the ecosystem may have different kinds of behavior. The main conclusions are depicted in bifurcation diagrams in the *l-h* plane, for fixed values of all the other parameters (Figure 3.1).

The line $l = h$ separates pure compensation from depensation behaviours. In pure compensation, for all biomass values, each unit added to the existing stock causes a decrease in the per capita growth rate. In other words we have a concave ecosystem production function. In depensation, for sufficiently low *N*, each unit added increases the per capita growth rate (convex-concave production function). If an ecosystem has depensation behaviour with the additional property of negative growth rates for some biomass levels, it is said to have critical depensation (Clark, 1976, p. 16). In this case, there is a certain threshold biomass stock level below which the ecosystem will become extinct.

We conclude that if feedbacks on carrying capacity are low enough (small *l* and high *h*) the ecosystem exhibits pure compensation. On the other hand, if feedbacks on carrying capacity are sufficiently high the ecosystem exhibits depensation and, for even higher feedbacks on carrying capacity, critical depensation. This reflects the greater intensity of the relations among populations of the ecosystem: at equal low biomass levels, ecosystems with higher bioengineering ability have lower growth rates.

3. The bioeconomic system

We consider the economic system composed by the aggregate of all firms that directly extract resources from an ecosystem with niche construction and export a resource flow to the wider economy. We call this economic system the extractive economy. This is an open economy that trades resources and investment flows with the wider economy for investment rents and consumption goods.

The state of the extractive economy is described by its state variables: ecosystem biomass, *N(t)*, and capital, *K(t)*. Decisions can be made at different levels, through the control variables: consumption rate, *c(t)*, and rate of extraction of environmental products or harvesting rate, *q(t)*. Once we choose to perform the optimisation at the macroeconomic level, it makes sense to consider that the analysis is performed in continuous time and all variables are continuous. This is because the discontinuities that result from individual decisions of harvesting or consumption overlap, being imperceptible at this scale.

The unperturbed ecosystem has a dynamics described in the previous section. Hence, the growth rate of the ecosystem is equal to the undisturbed regeneration function minus the extraction rate:

$$\frac{dN}{dt} = R(N) - q \,. \tag{4}$$

The extractive economy exports a flow of natural resources to the global economy with net economic revenue *V(q)*. This revenue depends on the supply of the ecosystem's resources, *q(t)*, since it is assumed that this flow is sufficiently large to alter the price of the resources. The net economic revenue function,

$V(q)$, has the following properties: $V \in C^2$, $V(0) = 0$, $V' > 0$, $V'' < 0$, which means that the net economic revenue function has positive but decreasing marginal benefits.

This economy has two sources of income, one resulting from the exported natural resources flow, $V(q)$, and the other resulting from the interest obtained from the capital investments in the global economy, dK, where d is the constant exogenous interest rate. This means that the extractive economy is small enough so that its investments in the global economy have no effect on the interest rate.

The proceeds from these two sources of income can either be directed to consumption or invested in accumulation of productive capital belonging to the extractive economy, dK/dt. Hence we have

$$\frac{dK}{dt} = dK + V(q) - c. \tag{5}$$

We assume that it is possible to define a utility function for this economy – citizens' preferences are identical and depicted by the representative consumer's utility function, $U(c)^2$ – and that a continuous and infinite overlapping succession of individuals will behave rationally so as to maximise their utility function throughout their lives. Hence, we are considering that future decisions feedback into the present to give an overall maximum discounted sum of the consumers' utility flow, $\int_0^\infty e^{-rt} U(c) dt$, where r is the discount or haste rate. Population is assumed to be constant, so the problem is solved on the behalf of a representative agent.

4. Optimal management with structural dynamics

After briefly presenting the different kinds of behaviour the ecosystem here considered may exhibit, we discuss its optimal management policies. It is important to stress that we give a special treatment to the solutions where the extraction rate is zero. Consequently, we have found some special cases of optimal policies that use zero extraction rates for some period of time. This kind of management policies is seldom found in the body of work in this area.

4.1. The optimal management problem

The problem that this economy faces consists in choosing the temporal trajectories for the consumption $c(t)$ and the extraction rates $q(t)$ in a context of interaction with the environment, in order to achieve the maximum inter-temporal utility benefit. Formally:

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[2] Utility is a continuous, twice differentiable, increasing, and strictly concave function of consumption rate.

$$\max_{c,q} \int_0^\infty U(c)e^{-rt}dt \text{ , s.t.}$$

$$\frac{dN}{dt} = R(N) - q, \tag{6}$$

$$\frac{dK}{dt} = \boldsymbol{d}K + V(q) - c, \tag{7}$$

$$N(t), K(t) \geq 0, \; c(t), q(t) \geq 0. \tag{8}$$

Assume that the extractive economy has fully known and fixed initial stocks $N(0) = N_0$, $K(0) = K_0$.

We use optimal control theory to characterize optimal solutions. Here the maximum is taken over the set of piecewise continuously differentiable functions $c(t), q(t) \geq 0$. In agreement with Pontryagin's maximum principle (Tu, 1994), the optimal candidate solutions maximise the current value Hamiltonian:

$$H(N, K, q, c, \boldsymbol{l}^N, \boldsymbol{l}^K) = U(c) + \boldsymbol{l}^N[R(N) - q] + \boldsymbol{l}^K[\boldsymbol{d}K + V(q) - c], \tag{9}$$

where the $\boldsymbol{l}^i$, are the co-state variables or shadow prices of capital $i = N, K$. The shadow prices are equal to the marginal value of the capital stock i at time t, i.e., if the stock level is reduced by one unit, its value at time t will be reduced by $\boldsymbol{l}^i(t)$. It is the price that produces the optimal exploitation of the resource if used in real markets. The Hamiltonian is the total rate of increase of total assets in units of the objective functional (utility units in this case), and the sum of the terms that have shadow prices is the value flow from investment in capital assets (Clark, 1976, p.104). Therefore, the shadow prices are multiplier factors that alter the units from capital units to units of the objective functional.

The optimal consumption and extraction rates must obey the first order conditions that optimise the Hamiltonian,

$$H_c = 0 \Leftrightarrow U' = \boldsymbol{l}^K \text{ or } c = 0, \tag{10}$$

$$H_q = 0 \Leftrightarrow \boldsymbol{l}^k V' = \boldsymbol{l}^N \text{ or } q = 0. \tag{11}$$

In this optimisation we are also interested in the possibility of corner solutions, hence we have to consider the maximisation of the Hamiltonian at the boundaries of the controllability domain, $q = 0$ and $c = 0$.

The first order conditions and the assumptions made on the utility and the net economic revenue imply that the shadow prices of natural capital and financial capital are both positive. The second order conditions for a local maximum require that all the pivots of the Hamiltonian Hessian matrix are negative.

The Hessian for this problem is a 2×2 diagonal matrix with $U^{''}(c)$ and $\mathbf{l}^K V^{''}(q)$ as elements. Since utility and net economic revenue are both assumed to have decreasing marginal gains, the pivots of the Hessian matrix are negative and conditions (10) and (11) are maximising conditions for the control variables.

Condition (10) is the usual optimal condition in economic growth models, and simply states that in the optimal strategy marginal benefits from consumption should equal marginal costs from the reduction in savings. To have the marginal benefit, $U^{'}(c)$, economic capital value must be reduced by $\mathbf{l}^K$. In other words, the marginal benefit from consumption must equal the capital value imputed by its future productivity; hence this condition depicts the inter-temporal effect associated with present or future consumption.

Condition (11) refers to the same effect, but now applied to the ecosystem – the marginal revenue from extraction of biological resources in utility units, should equal the marginal cost of depleting the resource, measured in loss of future productivity of the ecosystem. To have a marginal revenue in utility units[3], $\mathbf{l}^K V_q$, biological resource capital value should be reduced by $\mathbf{l}^N$.

Following Pontryagin's maximum principle the shadow prices for the optimal solution will evolve according to the following non-linear autonomous dynamical system:

$$\frac{1}{\mathbf{l}^N}\frac{d\mathbf{l}^N}{dt} + R^{'}(N) = \mathbf{r}, \qquad (12)$$

$$\frac{1}{\mathbf{l}^K}\frac{d\mathbf{l}^K}{dt} + \mathbf{d} = \mathbf{r}, \qquad (13)$$

with the usual transversality conditions,

$$\lim_{t \to \infty} e^{-rt}\mathbf{l}^K K = \lim_{t \to \infty} e^{-rt}\mathbf{l}^N N = 0. \qquad (14)$$

Equations (12) and (13) describe the dynamics of the marginal value associated with the accumulation process of the assets. As usual, in economic growth theory, these equations show that the global remuneration rate (income rate) from the assets must equal society's haste rate. Equation (13) shows the effect of investment in the global economy.

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[3] Or a marginal benefit from consumption due to the proceeds of extraction. So, this term shows how much the utility changes by changing one unit of the extraction rate.

Equation (12) is the Hotelling rule for a renewable resource. The influence on the remuneration rate of changes in ecosystem's bioengineering capability is implicit in the term $R'(N)$. This model predicts that the variation rate of the marginal value of the asset is now higher or lower than in traditional models with constant carrying capacity according to whether feedbacks on carrying capacity are positive or negative.

The optimal dynamics of consumption for interior solutions of (10) can be described by differentiating equation (10) with respect to time and using equation (13) to show that:

$$\frac{1}{c}\frac{dc}{dt} = \frac{\boldsymbol{d} - \boldsymbol{r}}{\boldsymbol{s}(c)}, \tag{15}$$

where $\boldsymbol{s}(c) = -(c/U_c)(dU_c/dc)$ is the elasticity of marginal utility relative to consumption.

The optimal dynamics of biomass extraction for interior solutions of (11), $q(t)$, is obtained by differentiating (11) with respect to time and substituting (12) and (13), yielding:

$$\frac{1}{V'(q)}\frac{dV'(q)}{dt} = \boldsymbol{d} - R'(N). \tag{16}$$

This condition implies that any positive disparity between the interest rate of the global economy and the marginal productivity of natural capital must be compensated by an increase in the value of the stock, which is done by increasing the price of the resource or reducing the flow of natural products to the global economy.

The dynamical system consisting of necessary conditions for the controls, $c(t)$ and $q(t)$, and the responses, $K(t)$ and $N(t)$, that maximises the Hamiltonian is composed of equations (6), (7), (15) and

$$\frac{1}{q}\frac{dq}{dt} = \frac{V'(q)}{V''(q)}\left(\boldsymbol{d} - R'(N)\right), \tag{17}$$

for interior solutions. For the optimal policy we must find the functions $c(t)$ and $q(t)$ such that these equations are satisfied for all times.

This system has 4 equations for 4 variables. However, the solution of (7) can be obtained after solving the remaining equations. Additionally, it is possible to solve separately equation (15) and the system of equations (6) and (17). Conceptually, this means that for this society the problem of optimal management of natural capital is independent of the optimal consumption problem. In Appendix I we present a demonstration of the separation of the optimisation problem.

This occurs because we have not considered nature services other than supply of resources, and assumed that the extractive economy does not affect the global economy's interest rate. In other words, this independent maximisation of utility and of extraction revenues is due to the fact that ecosystem

resources and services only enter the economy (contributing to utility) through the revenue function. As the optimal consumption problem for this society is independent of the natural resource management problem we may focus on the latter without loss of generality of the optimal policies derived.

Moreover, to clearly depict the corner solutions of the extraction problem it is necessary to study the system composed of the equations for the shadow prices and the state equation for the ecosystem. To do this, a new shadow price is defined as $l \equiv l^K / l^N$, which comes naturally from the optimisation of the ecosystem's revenue as shown in Appendix I.

Lemma 1

For every fixed N, the function

$$V'(q) = l \equiv j^{-1}(q)$$

is a differentiable and strictly increasing function of q. Hence it has a differentiable inverse $j(l) = q$.

Proof: From the first order condition (11) we get $V'(q) = l$, using $l \equiv l^K / l^N$. From the assumptions we have made on the net revenue function $V(q)$, it is obvious that it has a differentiable inverse. This implies that there exists a continuous function, $j(.)$, with the property $j'(l) < 0$, such that it is possible to rewrite condition (11) as $q = j(l)$. Q.E.D.

This lemma provides a way to exchange the state variable with the controls, making it possible to write the system (see Appendix I)

$$\frac{dN}{dt} = R(N) - j(l), \tag{18}$$

$$\frac{1}{l} \frac{dl}{dt} = d - R'(N). \tag{19}$$

The corner solution is now obvious ($j(l) = 0$) and can be depicted in a $N - l$ phase space.

In the following sections we describe the optimal policies for the management of an ecosystem considering three different scenarios for ecosystem dynamics: pure compensation, depensation and critical depensation.

We shall present the optimal policies using geometrical devices like phase diagrams, where the axes are the ecosystem biomass, N, and its modified shadow price, l, which is now in capital units. Note that, the shadow price $l(t)$ is inversely related to the extraction rate $q(t)$. We have decreasing strictly positive

extraction rates for increasing values of the shadow price, reaching a zero extraction rate for $l \geq V'(0)$.

Moreover note that we have imposed the restriction $N \geq 0$ on the phase space. So, the sections of optimal trajectories that lie entirely in the interior of our phase space region, i.e. $N > 0$, satisfy the usual maximum principle. The sections of optimal trajectories that lie entirely on the boundary of this region, $N = 0$, satisfy Theorem 22 of Pontryagin et al. (1962). Finally, every pair of adjoining sections of an optimal trajectory, one of which lies in the interior and the other lies on the boundary, satisfy the junction condition in Pontryagin et al. (1962). We use this in Appendix III.

4.2. Pure compensation

In figure 4.1 we have the case of an ecosystem with pure compensation. The bioeconomic system possesses one optimal equilibrium solution $N = N^*$ which is a saddle point (Appendix II). As shown in Appendix III the only possible optimal solutions are those that have initial conditions on the one-dimensional stable manifold that extends for all values of N (global maximum), converging to the steady state, as depicted in figure 4.1.
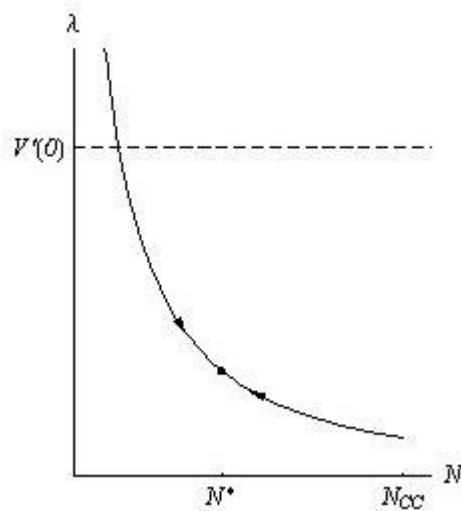

Figure 4.1 – Phase diagram with the optimal trajectories for the extraction revenues maximisation problem in the case of an ecosystem with pure compensation behaviour.

So, the optimal policy implies that the ecosystem will be harvested up to the point, at which its marginal net productivity –which is the rate of return from holding the ecosystem – is equal to the interest rate of the economy, $d = R'(N^*)$. This is the usual golden rule of marginal productivity used to derive simple management policies for renewable resources (Clark, 1976). As we will see below, the policies derived in order to achieve the capital level of the golden rule are not optimal in the case of ecosystems with depensation and critical depensation.
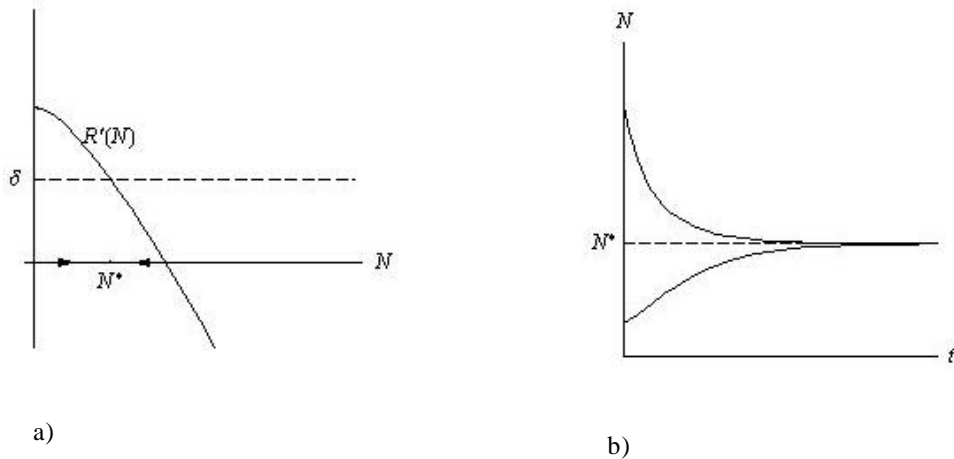
a)   b)

Figure 4.2 – **a)** Graphical representation of the solution of $d = R^{'}(N)$ for an ecosystem with pure compensation behaviour. **b)** Optimal stock paths N(t) for two different initial conditions.

In terms of management policies, the marginal productivity rule states that, if the interest rate exceeds the rate of return from holding the biomass constant, it is more profitable to harvest the resource at a rate higher than the regeneration rate and invest the proceeds in the global economy. In particular, if $d \geq R^{'}(0)$ it follows that extinction is the optimal policy (Clark, 1976). On the other hand, the ecosystem will continue to grow or regenerate if that choice yields a greater net present value than immediate harvesting without regeneration. Hence, a renewable resource is a relatively poor investment if its natural regeneration rate is less than the rate of return of investing in capital in the global economy.

Figure 4.2 shows the approach to the bioeconomic equilibrium N^{*}. This solution corresponds to following the one-dimensional stable manifold in figure 4.1, and has the stock-level path depicted in figure 4.2 b). Numerically computing the separatrices show in figure 4.1 we have the optimal feedback control law for the extraction of ecosystem products. This, as seen in figure 4.2 b) is an optimal approach path that is a gradual approach, engendered by market reactions to the harvest rate (Clark, 1976).

4.3. Depensation

If we are exploiting an ecosystem with depensation behavior, we expect that the optimal policy should be different from that of an ecosystem with less niche construction capability (pure compensation). In particular, we expect this to happen for low levels of the ecosystem's biomass, since it is for low biomass levels that the main qualitative differences appear in the marginal growth rates. This can be seen by comparing figure 4.2 a) with figure 4.3.

In this case, there are now two steady states, one stable and another unstable. In appendix II we show that one is a saddle-point and the other may be an unstable focus or node depending on the bioengineering capability of the ecosystem relative to the interest rate.
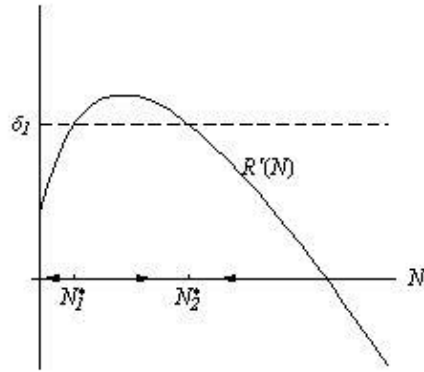
Figure 4.3 – Graphical representation of the solutions of $d_1 = R'(N)$ for an ecosystem with depensation behavior. In this case there is a zone of optimal extinction of the ecosystem.

From figure 4.3, using the golden rule of marginal productivity we can still draw some general ideas about the optimal policy for the management of an ecosystem with depensation behavior. If $N_0 > N_2^*$ then the optimal solution would be, as for an ecosystem with pure compensation, to harvest it at a rate higher than its regeneration. Consequently the ecosystem biomass would decrease, approaching the equilibrium biomass N_2^*. If the ecosystem has a higher marginal growth than the interest rate it is more profitable to harvest the ecosystem at a rate lower than its regeneration, so that its biomass approaches the equilibrium biomass. In this case, this leads to the prediction of optimal extinction policies for low ecosystem biomass levels. However, when the initial state of the ecosystem is near the unstable steady state, Pontryagin's maximum principle does not provide a unique optimal policy, as we will show, and the application of the golden rule fails to yield optimal policies.

In appendix III we prove that the optimal candidate solutions are those depicted in figure 4.4. Near the focus, the optimal trajectories oscillate, making it possible, for a given N_0, the existence of multiple optimal initial extraction rates. Each of these is a local maximum of the value function

$$W(q) \equiv \max_q \int_0^\infty V(q)e^{-dt}dt \text{ subject to } N(0) = N_0.$$

The decision of what extraction rate to choose should then be made in terms of revenue gains (i.e. choosing the global maximum from a set of local maxima). To choose global optimal candidates among these we use the criterion devised by Skiba (1978) and generalized in Brock and Starrett (2003). Hence, even though the golden rule of capital accumulation is widely accepted and used intuitively for renewable resource management, here we see that it cannot be generalized to an ecosystem with depensation and critical depensation behavior. The optimal feedback control law must be derived by solving equations (18) and (19), with $q = j(l)$.

There exists, now, more than one locally stable manifold satisfying all transversality and necessary conditions. Our strategy is, as in Brock and Starrett (2003) or Wagener (2003), to use the Hamilton-Jacobi-

Bellman (HJB) equation to compute a collection of 'candidate' value functions $W_i(\overset{*}{q}; N_0)$ for every N_0. The following lemma is taken from Skiba (1978) (proposition 2).

Lemma 2:

If (N, q^*) is an optimal trajectory starting at (N_0, q_0^*), then the following equality holds:

$$W(q^*; N_0) \equiv \int_0^\infty V(q^*) e^{-dt} dt = \frac{1}{\boldsymbol{d}} H(N_0, q_0^*, \boldsymbol{l}_0^*),$$ (20)

where $H(N_0, q_0^*, \boldsymbol{l}_0^*) = V(q_0^*) + \boldsymbol{l}_0^*[R(N_0) - q_0^*]$, and $q_0^* = \boldsymbol{j}(\boldsymbol{l}_0^*; N_0)$.

Note that, as stressed by Wagener (2003) in the context of lake management, the value function W is defined for all starting points on optimal trajectories.

Given this, the globally optimal value function is given by

$$W(\overset{*}{q}; N_0) = \max_i [W(\overset{*}{q}; N_0)],$$ (21)

where the index i represents different locally optimal trajectories, and the criterion for the comparison of the different value functions depending on q_i^* is the following.

Lemma 3: (Candidate value function comparison)

Consider two optimal extraction rates q_1^*, q_2^* implying two optimal candidate value functions $W(q_1^*)$ and $W(q_2^*)$, evaluated at any chosen N_0. If

$$\boldsymbol{l}_2^* dN_1/dt \geq \boldsymbol{l}_1^* dN_1/dt$$ (22)

where $dN_i/dt = R(N_0) - q_i^*$; then $W(q_2^*) \geq W(q_1^*)$.

Proof: Applying lemma 2 for the comparison of the two value functions we have

$$\boldsymbol{d}[W(q_2^*) - W(q_1^*)] = V(q_2^*) - V(q_1^*) + \boldsymbol{l}_2^* dN_2/dt - \boldsymbol{l}_1^* dN_1/dt$$

Using inequation (22), we get $\boldsymbol{d}[W(q_2^*) - W(q_1^*)] \geq V(q_2^*) - V(q_1^*) + \boldsymbol{l}_2^* [dN_2/dt - dN_1/dt]$. From equation (6) the right hand side of the former inequality becomes $V(q_2^*) - V(q_1^*) + \boldsymbol{l}_2^* [q_2^* - q_1^*]$.

Knowing that $V(q)$ is concave and $l_2^* = V'(q_2^*)$, we have $V(q_2^*) - V(q_1^*) + l_2^*[q_2^* - q_1^*] \geq 0$. Q.E.D.

This lemma is equivalent to proposition 5 of Brock and Starrett (2003) or Lemma 4 of Wagener (2003).

From figure 4.4 we obtain the same management policies as the ones derived from figure 4.3 for $N_0 > n$. The same is true for the discussion of the existence of optimal extinction using figure 4.3, i.e., for $N_0 < m$, the optimal candidate management policy is to follow the unstable one-dimensional manifold that approaches $N = 0$ asymptotically. The existence of optimal trajectories towards the saddle point or towards $N = 0$ implies the existence of a Skiba point (Brock and Starrett, 2003; Wagener, 2003). This is the initial state where the long run steady states for the optimal programs change.

So, applying lemma 3 to find the optimal candidate solutions for all values of ecosystem biomass in the case of convex-concave ecosystem production functions we have the following lemma.

Lemma 4:

For the exploitation of an ecosystem with a convex-concave production function, there is a unique Skiba point s in the interval $[m, n]$ such that the saddle point is the long run optimal candidate solution for $N_0 > s$ and the optimal extinction of the ecosystem is the long run optimal solution for $N_0 < s$.

Proof: This lemma is obvious since for $N_0 > n$ the saddle manifold must be optimal, the extinction manifold must be optimal for $N_0 < m$ and by continuity of the solution there must be a switch point inside $[m, n]$. Q.E.D.

So, to calculate the Skiba point we only need to compute the HJB equation as in equation (21) for the two one-dimensional manifolds (saddle and extinction) that are optimal candidates according to Lemma 3 and the N_0 where the lines $W(l_i^*; N_0)$ intersect is the Skiba point, s.

The optimal policies after using Lemma 3, calculating the Skiba point using equation (21) and using Lemma 4 are depicted in figure 4.4 b). Notice that the sections of the optimal trajectory on the boundary of the controllability domain appear naturally. For instance, if $s < N_0 < n$ the optimal trajectory has a period of zero extraction rates followed by the gradual approach to the saddle point extraction rate.

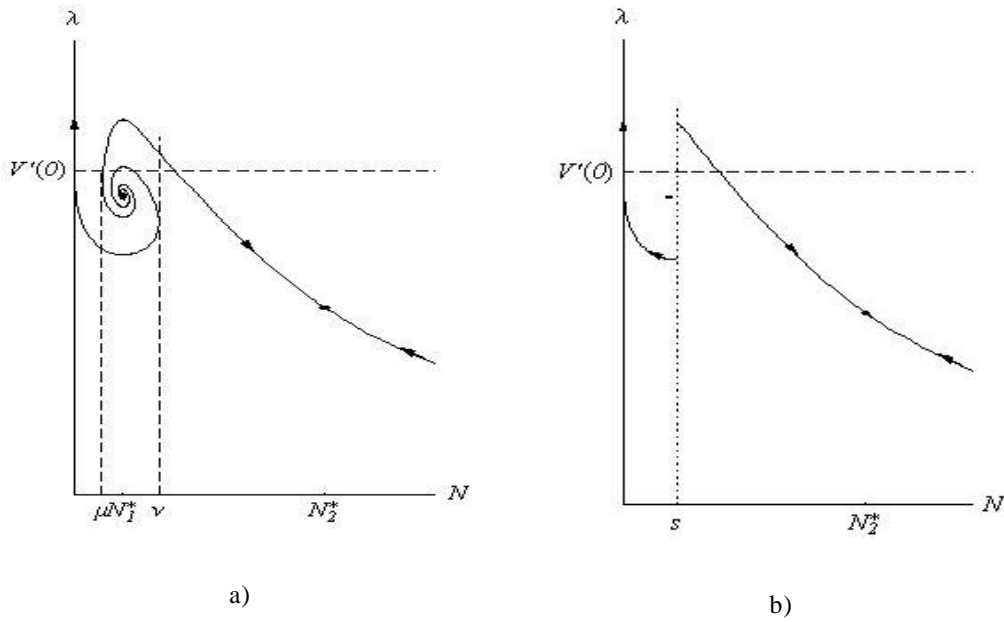**Figure 4.4 – a)** Phase diagram with the optimal candidate solutions for an ecosystem with depensation, showing the interval $[\boldsymbol{m,n}]$ containing the Skiba point. **b)** Phase space depicting the optimal trajectories after applying Lemma 3.

A direct implication of lemma 4 is the following generalization of the golden rule of marginal productivity for convex-concave ecosystem production functions.

Lemma 5: (Generalized golden rule of marginal productivity)

Consider the conditions of lemma 4.

If $s < N_1^*$ then the golden rule is applied for every N except in the interval $[s, N_1^*]$, where the optimal policy is to let the ecosystem regenerate.

If $s > N_1^*$ then the golden rule is applied for every N except in the interval $[N_1^*, s]$, where the optimal policy is to harvest at a rate higher than its regeneration.

If $s = N_1^*$ then the golden rule is applied for every N.

This Lemma is an important remark due to the wide acceptability of golden rule derived policies, and the high probability of encountering a renewable resource with a convex-concave regeneration function in management problems.

The existence of a Skiba point indicates that the long-term behavior of the bioeconomic system will be history dependent: in our case, this means that according to the conditions prevailing in the first phases of development, the ecosystem is led to the saddle point or towards extinction. Small changes of initial

values near the Skiba point have dramatically different responses, one leading to the sustainable conservation of the ecosystem and the other leading to its extinction.

An ecosystem needs to be a high productivity system in order to be maintained by the owners. It is important, however, to stress that the optimal extinction of an ecosystem involves costs that are not considered in this model, such as increasing cost of extraction due to scarcity of resources, social costs associated with environmental functions and other externalities. Still, optimal extinction may be a real policy option for the management of natural resources.

Moreover, this only depends on the productivity of the ecosystem relative to the interest rate and the initial level of the ecosystem biomass. If the interest rate has a sudden increase (more economic pressure on the ecosystem), the realm of optimal extinction increases, as can be seen from figure 4.3 and 4.4. However, both pure compensation and depensation ecosystems may be prevented from optimal extinction if the interest rate becomes sufficiently low. Accordingly, if the ecosystem has depensation behavior and if the interest rate is lower than $R^{'}(0)$, the optimal management policies will be the same as in the case of pure compensation behavior.

4.4. Critical depensation

The candidate optimal trajectories for the management problem with critical depensation are depicted in figures 4.7 and 5.2.6 for higher ecosystem bioengineering capability. The ecosystem threshold biomass N_{tr} is where the dashed curve crosses the line $I = V^{'}(0)$. The Skiba point, s, for figure 4.7 is depicted and was computed as in the depensation case. Applying Lemma 3 to the case of figure 5.2.6 it is known that the Skiba point coincides with N_{tr}.
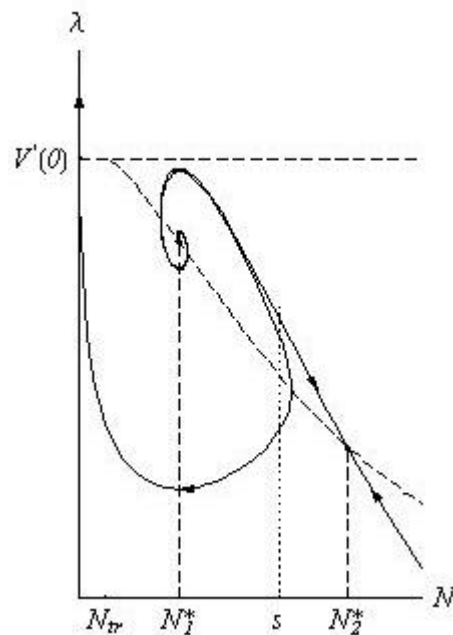

Figure 4.7 – Phase diagram with the optimal trajectories for an ecosystem exhibiting critical depensation.

If the ecosystem has critical depensation behavior, the optimal system exhibits all the phenomena encountered in the depensation case, as well as an additional phenomenon: irreversibility. All the lemmas used in the previous section hold for critical depensation. However, for pure compensation and depensation there are certain interest rates that prevent the existence of history dependence, whereas in critical depensation there exists Skiba points for bioengineering capability for which $d = R^{'}(N)$ has solutions. In fact, in the case of critical depensation there are always initial conditions for which it is optimal to extinguish the ecosystem for any interest rate. This can be seen in figure 4.8. This shows that it is only in special cases that management policies are the same for ecosystems with different self-bioengineering capability.

Now, comparing, for the same biomass, ecosystems with the different bioengineering capability, the conclusion, as expected, is that extracting and exporting is still a good investment for higher interest rates or, for the same interest rate, the equilibrium population corresponding to the saddle point is greater. This can be seen from figure 4.9, where we have plotted the marginal growth curves for two ecosystems, one with pure compensation and the other with depensation behaviour due to higher niche construction. This means that when the system loses bioengineering species it also loses productivity and competitiveness for the global economy. Ecosystems' niche construction potentiates the creation of new ecosystem biomass, increasing the surplus from holding the resources, and consequently augmenting the range for economic profitability. On the other hand, for low biomass levels the ecosystem with a lower bioengineering capability has a greater surplus.
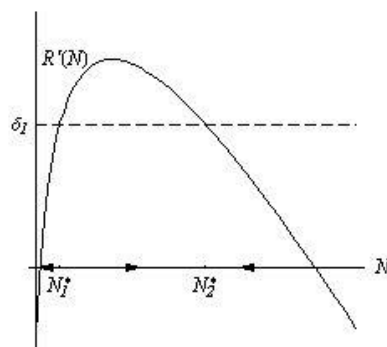

Figure 4.8 – Bioeconomic equilibria with an ecosystem with critical depensation behaviour. In this case there is always a zone of optimal extinction ecosystem.

The autocatalytic relations between the actual biomass and ecosystem carrying capacity creates extreme states of productivity for the ecosystem, whether they are of very high productivity or very low.
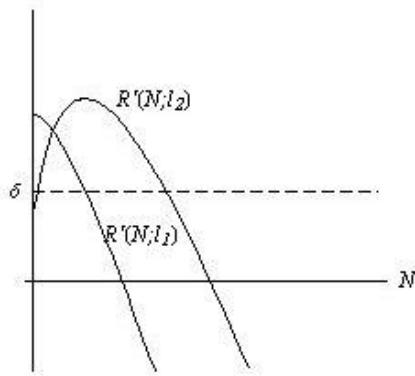
Figure 4.9 – Comparison of ecosystems with different bioengineering capabilities. In this case, according to figure 3.1a) we have $l_1 < l_{crit}^{(1)} < l_2$.

5. Optimal policies bifurcation diagram

As seen above, depending on the relative values of the parameters of the model, the optimal policies for the ecosystem management are different. We sketch this changes in what we call optimal policies bifurcation diagrams (Fig. 5.1). These diagrams represent different optimal policies in various *l-h* diagrams for different relative values of CC_l, as in accordance with the ecological bifurcation diagrams. The line separating *SP* from *E-SP* is a line of saddle-node bifurcations points, and the line separating *E* from *E-SP* is a line of heteroclinic bifurcations.
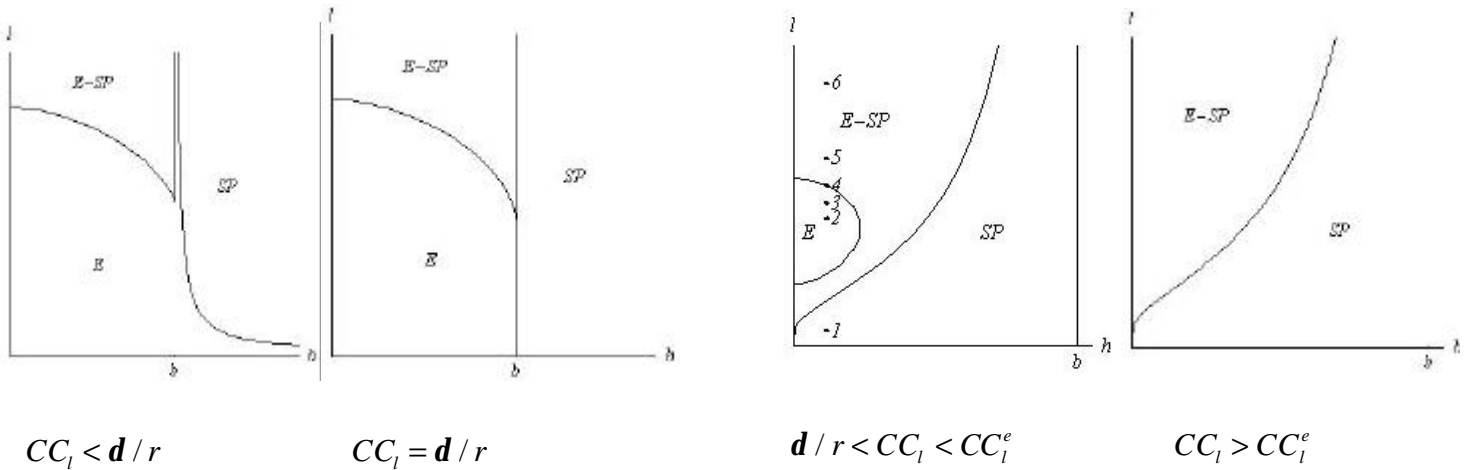

$$CC_l < d/r \qquad CC_l = d/r \qquad d/r < CC_l < CC_l^e \qquad CC_l > CC_l^e$$

Figure 5.1 – Optimal policies bifurcation diagrams. **a)** *SP* means Saddle point directed policies. *E* means optimal extinction policies. *E-SP* means that the system has a both optimal policies depending on the initial ecosystem biomass level.
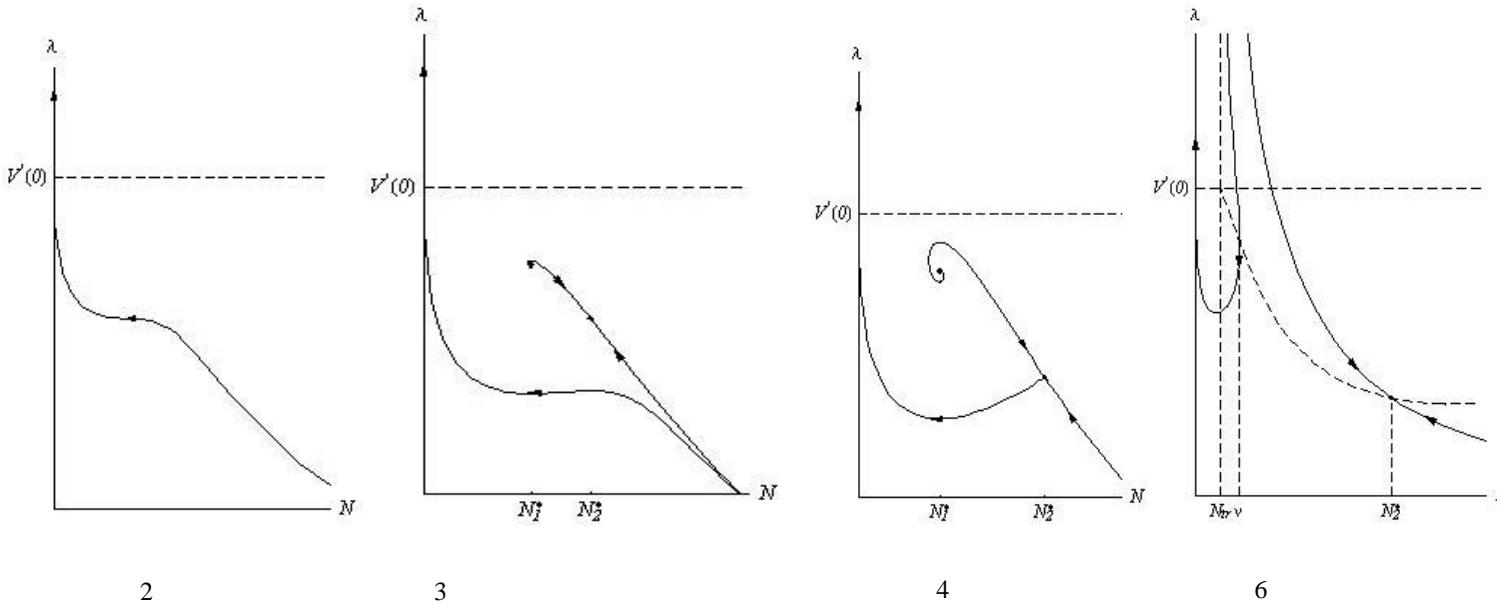
2   3   4   6

Figure 5.2 – Phase portraits for different parameter points in figure 5.1.

The optimal phase portrait of point 1 in figure 5.1 is figure 4.1, and for point 5 is figure 4.7. For the phase portrait 3 and 4 we have represented trajectories that are not optimal. For figure 5.2.3 the only optimal trajectory is the optimal extinction path. This is known by applying Lemma 3 to any point higher than N_2^* and using the connectedness property of optimal paths. The phase portrait 4 represents a heteroclinic bifurcation. Finally, phase portrait 6 represents the case where the equilibrium N_1^* vanishes by crossing the line $l = V'(0)$. This happens for high values of l. Nevertheless, applying Lemma 3 to the interval $[N_{tr}, \boldsymbol{n}]$ we know that the optimal trajectory is the saddle path. So, for $N < N_{tr}$ the optimal policy leads the ecosystem to extinction, and the optimal policy leads to the saddle point for $N > N_{tr}$.

6. Acknowledgments

7. Concluding remarks

In this work we have characterized and discussed the optimal management policies for an ecosystem with niche construction along ecological succession. For this, we have used a phenomenological model for the ecosystem dynamics that grasps the dependence of the ecosystem productivity on its ecosystem engineers.

We performed a dynamical optimisation of an extractive economy exploiting this ecosystem. The main conclusion is that the optimal policies will, in general, depend on the niche construction feedbacks of the ecosystem. Only in the case of the interest rate being lower than $R^{'}(0)$ are pure compensation and depensation ecosystems managed with the same type of optimal policies. Moreover, the usual golden rule of marginal productivity of renewable resources has been generalised to derive optimal policies for convex-concave ecosystem production functions. For ecosystems with depensation or critical depensation behaviours we show the existence of a Skiba point. Hence, there is history dependence in this bioeconomic model.

Generally, we can conclude that an ecosystem with high bioengineering capability has a wider range of profitability than an ecosystem with lower bioengineering capability. On the other hand, it also has a higher realm of optimal extinction. So, managers must balance the need for high productivity of the ecosystem with its high risk of extinction.

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Appendix I – Corner solutions and separation of problems

As mentioned in the text, the system we obtained can be viewed as maximizing two separate problems. One is the problem of maximization of utility using the consumption rate and the other is the maximization of economic revenue using the natural resource extraction rate. In a more formal perspective, if we could define the problems that give rise to the optimal system for the global problem we would have demonstrated the separability of the optimization problems.

Formalizing the two problems, we have for the utility maximization,

$$\max_{c} \int_0^\infty U(c)e^{-rt}dt \text{ , s.t.}$$

$$dK/dt = \boldsymbol{d}K + V(q) - c \,. \tag{A1.1}$$

The current value Hamiltonian is

$$H(K, c, \boldsymbol{l}^{K}) = U(c) + \boldsymbol{l}^{K}[\boldsymbol{d}K + V(q) - c], \tag{A1.2}$$

and the shadow price equation is

$$\frac{1}{\boldsymbol{l}^{K}}\frac{d\boldsymbol{l}^{K}}{dt} + \boldsymbol{d} = \boldsymbol{r} \,, \tag{A1.3}$$

with the transversality condition

$$\lim_{t \to \infty} e^{-rt} \mathbf{1}^K K = 0,$$

which are the same as the equations derived from the original optimization problem. The first order condition is $H_c = 0 \Leftrightarrow U'(c) = \mathbf{1}^K$, from which equation (15) can be derived.

Now, for the maximization of the ecosystem's rent we have,

$$\max_q \int_0^\infty V(q)e^{-dt}dt \text{, s.t.}$$

$$dN/dt = R(N) - q. \tag{A1.4}$$

The functional objective now represents a sum of financial capital flows discounted using the rate of interest of the global economy. The current value Hamiltonian function is

$$H(N, q, \mathbf{1}) = V(q) + \mathbf{1}[R(N) - q], \tag{A1.5}$$

where the shadow price, $\mathbf{1}$, is the marginal value of the ecosystem in financial capital units, so it must have units of financial capital per 'ecosystem capital units'. The shadow price equation is

$$\frac{1}{\mathbf{1}} \frac{d\mathbf{1}}{dt} = \mathbf{d} - R'(N). \tag{A1.6}$$

with the transversality condition given by

$$\lim_{t \to \infty} e^{-dt} \mathbf{1} N = 0.$$

Defining $\mathbf{1} \equiv \mathbf{1}^K / \mathbf{1}^N$, we have

$$\frac{d\mathbf{1}}{dt} = \frac{1}{\mathbf{1}^K} \frac{d\mathbf{1}^N}{dt} - \frac{\mathbf{1}^N}{\mathbf{1}^K} \frac{1}{\mathbf{1}^K} \frac{d\mathbf{1}^N}{dt}. \tag{A1.7}$$

Substituting this and (A1.3) in (A1.6), we obtain

$$\frac{1}{\mathbf{1}^N} \frac{d\mathbf{1}^N}{dt} + R'(N) = \mathbf{r}, \tag{A1.8}$$

which corresponds to the shadow price equation derived from the original optimization problem. The first order condition is $V'(q) = \mathbf{1}$, which leads to equation (17), proving that the optimal system for the original problem is equivalent to having the two above-mentioned dynamical systems.

To make the corner solutions appear naturally in phase space we have to use lemma 1 with the state equation (A1.4) and equation (A1.6). So, the system to be analyzed is:

$$\frac{dN}{dt} = R(N) - \boldsymbol{j}\,(\boldsymbol{l})\,, \tag{A1.9}$$

$$\frac{1}{\boldsymbol{l}}\frac{d\boldsymbol{l}}{dt} = \boldsymbol{d} - R^{'}\,. \tag{A1.10}$$

To obtain the system corresponding to the corner solutions we simply have to consider a zero extraction rate, or $\boldsymbol{j}\,(\boldsymbol{l}) = 0$ in equation (A1.9). So, if we are considering the phase space N-$\boldsymbol{l}$ the separation of the interior from the corner solutions corresponds to $\boldsymbol{l} = V^{'}(0)$, from Lemma 1. So, the next question is whether the interior and corner solutions verify a junction condition imposing that they are continuously differentiable when $\boldsymbol{l} = V^{'}(0)$.

To study the differentiability of solutions we have to look at the derivative of the trajectories at the junction line,

$$\frac{d\boldsymbol{l}}{dN} = \frac{\boldsymbol{d} - R^{'}(N)}{R(N) - \boldsymbol{j}\,(\boldsymbol{l})}\,. \tag{A1.11}$$

Observing that, either, when $\boldsymbol{j}\,(\boldsymbol{l}) \to 0^{+}$ or $\boldsymbol{j}\,(\boldsymbol{l}) \to 0^{-}$, $d\boldsymbol{l}/dN \to (\boldsymbol{d} - R^{'})/R$ we conclude that the solutions are continuous and differentiable at $\boldsymbol{l} = V^{'}(0)$.

Appendix II – Qualitative characterization of equilibria

Consider the nonlinear system $dx/dt = f(x)$. Using Taylor expansion about some equilibrium x^{*}, we have

$dx/dt = Ax + \boldsymbol{z}\,(x)$, where

$$A \equiv Df(x)_{x=x^{*}} \equiv \begin{pmatrix} \partial f_{1}/\partial x_{1} & \cdots & \partial f_{1}/\partial x_{n} \\ \vdots & \ddots & \vdots \\ \partial f_{n}/\partial x_{1} & \cdots & \partial f_{n}/\partial x_{n} \end{pmatrix}_{x=x^{*}}\,,$$

and $\boldsymbol{z}\,(x)$ is such that $\lim_{x \to x^{*}} \boldsymbol{z}\,(x) = 0$. The system $dx/dt = Ax$ is the linearized system.

Theorem A2.1 (Linearization theorem of Hartman & Grobman, in Tu, 1994). Let the nonlinear dynamic system $dx/dt = f(x)$ have a hyperbolic equilibrium point x^*. Then, in the neighborhood of $x^* \in \mathbb{R}^n$ the phase portraits of the nonlinear system and its linearization are equivalent.

This theorem simply states that provided $\mathrm{Re}(\boldsymbol{a}_i) \neq 0$ then the nonlinear and linear systems are qualitatively equivalent near the equilibrium point.

Applying the linearization theorem to our system,

$$dN/dt = R(N) - \boldsymbol{j}\,(\boldsymbol{l})\,, \tag{A2.1}$$

$$\frac{1}{\boldsymbol{l}}\frac{d\boldsymbol{l}}{dt} = \boldsymbol{d} - R^{'}(N)\,. \tag{A2.2}$$

we have that

$$A = \begin{pmatrix} R^{'}(N) & -\boldsymbol{j}^{'}(\boldsymbol{l}) \\ -\boldsymbol{l}R^{''}(N) & \boldsymbol{d} - R^{'}(N) \end{pmatrix}_{(N^*, I^*)} = \begin{pmatrix} \boldsymbol{d} & -\boldsymbol{j}^{'}(\boldsymbol{l}^*) \\ -\boldsymbol{l}^*R^{''}(N^*) & 0 \end{pmatrix}.$$ Now, to find the eigenvalues

$\boldsymbol{a}_i$ of A we solve $\det(A - \boldsymbol{a}I) = 0$. This is equivalent to solving the characteristic polynomial

$$P(\boldsymbol{a}; N^*) \equiv \boldsymbol{a}^2 - \boldsymbol{d}\boldsymbol{a} + \left(R(N^*) + 1\right)R^{''}(N^*) = 0\,. \tag{A2.3}$$

We will now make two propositions concerning the types of steady states of our system. We use geometrical devices for the proofs in order for it to be more intuitive. However, the detailed derivation of the figures used is made in Mota et al. (2004).

Proposition A2.2 – Let the system comprised of equations (21) and (22) have one equilibrium point N^*. Then N^* is a saddle point.

Proof. N^* being a saddle point is equivalent to having $\boldsymbol{a}_1 < 0 < \boldsymbol{a}_2$ (Tu, 1994). From $P(\boldsymbol{a}; N^*)$ we know that the coordinate of its vertex is $(\boldsymbol{d}/2, \Delta - \boldsymbol{d}^2/4)$, where $\Delta \equiv (R+1)R^{''}$. So, for different equilibria, ? is the only variable expression, and its sign is controlled by $R^{''}$. The solutions of $\boldsymbol{d} - R^{'} = 0$ are depicted in figure A2.1 for the case of depensation and compensation and for different interest rates. For critical depensation there are always two steady states (see figure 4.8), so we may focus on the depensation case without loss of generality. We can see from figure A2.1 that in the case of one equilibrium, $\boldsymbol{d} = \boldsymbol{d}_2$, we have $R^{''}(N^*) < 0$. So $\Delta < 0$ or $P(0; N^*) < 0$, which, combined with the position of the vertex of the characteristic polynomial, implies that there is one positive and one negative solution of $P(\boldsymbol{a}; N^*) = 0$. This is the case of a saddle point. Q.E.D
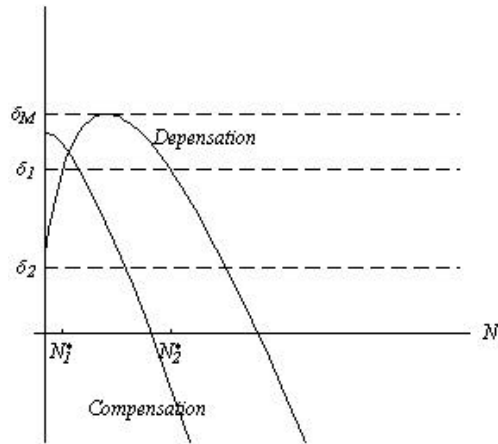
Figure A2.1 – Graphical solution of $d = R'(N)$ in the case of compensation and depensation, for several interest rates.

Proposition A2.3 – Let the system comprised of equations (A2.1) and (A2.2) have two equilibrium points $N_1^* \neq N_2^*$. Then one is a saddle point and the other is an unstable focus or an unstable node. Furthermore, there is a saddle-node bifurcation for $d = d_M$ (figure A2.1).

Proof. If there are two equilibrium points, $d = d_1$ for instance, without loss of generality, then (as seen from figure A2.1) we know that $R''(N_1^*) > 0 > R''(N_2^*)$. This, as the proof of the last theorem states, suffices to show that the equilibrium at N_2^* is a saddle point. Using the same argument for N_1^*, we can conclude that N_1^* is an unstable focus for low d, becomes an unstable node for increasing d and later a saddle-node bifurcation occurs for $d = d_M$. The characteristic polynomial for the unstable node and unstable focus cases are represented in figure A2.2. We know that they are unstable since the real part of the eigenvalues is given by $d / 2 > 0$. When $d = d_M$, the linearization of the system is not valid since there is an eigenvalue that is zero (bifurcation point). Q.E.D.
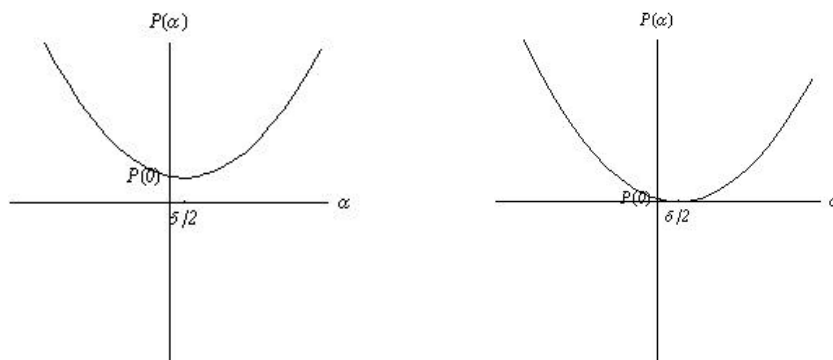
Figure A2.2 – Characteristic polynomial for the unstable focus and the unstable node. In the cases depicted we have the eigenvalues of A: a) $a_1 = 0.1 - i0.393$ and $a_2 = 0.1 + i0.393$; b) $a_1 = 0.124$ and $a_2 = 0.141$.

Appendix III – Using transversality conditions

Since each phase plane diagram gives necessary conditions for the trajectories, not all of them are optimal; hence we have to decide what trajectories should be considered a solution of the optimisation.

Pure compensation

The phase portrait of the system composed of equations (18) and (19) for pure compensation growth is depicted in figure A3.1. The bioeconomic system possesses one steady state $N = N^*$ which is a saddle point (Appendix II). In the interior of the phase space there are four kinds of trajectories: the equilibrium; the stable and the unstable separatrices of the saddle point; the trajectories that lead the ecosystem to extinction; and the trajectories that approach N_{CC} for $t \rightarrow +\infty$.
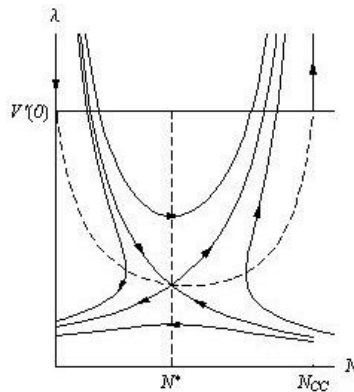

Figure A3.1 – Phase portrait of the system of equations (18) and (19) for a pure compensation ecosystem production function.

In our phase space, the boundary for the ecosystem biomass is $N = 0$. The jump condition in Pontryagin et al. (1962) implies that the optimal trajectory remains smooth at the junction point. So, the trajectories that lead the ecosystem to extinction in the case of compensation are not optimal since they are not smooth at $N = 0$. This also holds in the cases of depensation and critical depensation. This is in accordance with the proof presented in Blanchard and Fischer (2000; p75) for ruling out explosive paths in the Ramsey model.

In the case of trajectories that are increasing in l for $t \rightarrow +\infty$, if they do not verify the transversality condition,

$$\lim_{t\to\infty} e^{-dt}\, \mathbf{l}\, N = 0, \tag{A3.1}$$

they are not solutions of the optimisation problem. For *t* near infinity, we know that $N \approx N_{CC}$ from the dynamics of the ecosystem biomass equation (18), and $d\mathbf{l}/dt \approx \mathbf{l}(\mathbf{d}+\mathbf{x})$, where $\mathbf{x} = -R^{'}(N_{CC}) > 0$, as we know from equation (3) and can be seen in figure 4.2 a). Integrating, we have $\mathbf{l} \approx e^{(\mathbf{d}+\mathbf{x})t}$, and substituting in the condition (A3.1) we obtain,

$$\lim_{t\to\infty} e^{\mathbf{x}t} N_{CC} = +\infty , \tag{A3.2}$$

which violates the transversality condition. Therefore the candidate optimal trajectories are depicted in figure 4.1.

Depensation

The phase portrait for an ecosystem with depensation growth is showed in figure A3.2. The results of the previous section for pure compensation growth still hold for depensation growth except for the trajectory that approaches $N = 0$ asymptotically.

Applying transversality condition (14) we know from equation (18), and can be seen in figure A.3.2, that if *t'* is higher than some t^{*}, for which we have $N(t^{*}) = 0$, then $N(t') = 0$. This implies that the transversality condition is verified, and the trajectory is a candidate optimal trajectory. So, the optimal candidate solutions for the depensation case are depicted in figure 4.4.
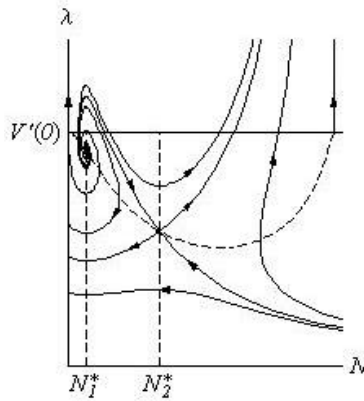

Figure A3.2 – Phase portrait of the system of equations (18) and (19) for a depensation ecosystem production function.

Critical depensation

The phase portrait for an ecosystem with depensation growth is showed in figure A3.3. In order to obtain the candidate optimal trajectories for the exploitation of an ecosystem with critical depensation we can use the results obtained for compensation and depensation. So, we need only to prove whether the

trajectories that asymptotically tend to zero with no extraction rate are candidate optimal trajectories or not. Following these trajectories, for t near infinity, $N(t)$ approaches zero and $d\mathbf{1}/dt \approx \mathbf{1}\,(\mathbf{d}+\mathbf{z})$, where $\mathbf{z} = -R(0) > 0$, as know from equation (2) and depicted in figure A.3.3. Integrating, we have $\mathbf{1} \approx e^{(\mathbf{d}+\mathbf{z})t}$. We may, now, use an approximation of the trajectories of interest near zero ecosystem biomass. For this purpose we linearize the function $R(N)$ in the neighborhood of zero as,

$$R(N) = R(0) + R'(0)N + o(N^2).$$ (A3.3)

This can be rewritten as $R(N) = -\mathbf{z}\,N$, from which we know that $N(t) = e^{-zt}$. Substituting this in the transversality condition we get,

$$\lim_{t\to\infty} e^{-xt} e^{xt} = 1,$$ (A3.4)

implying that the trajectories are not candidate optimal policies. This makes sense, since it would not be optimal to stop the extraction rate for some positive value of ecosystem biomass, for if the ecosystem is going to extinction then it is better to extinguish it by using some positive extraction rate and obtain revenues from it. Thus, the optimal candidate solutions for the critical depensation case are those depicted in figure (4.7).
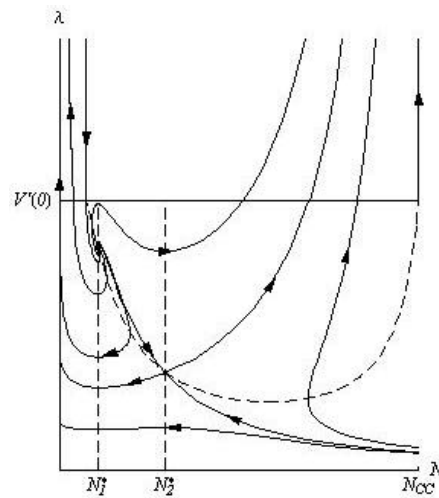

Figure A3.3 – Phase portrait of the system of equations (18) and (19) for a critical depensation ecosystem production function.