

Management Challenges for Multiple-Species Boreal Forests

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NOTA DI LAVORO 106.2003

DECEMBER 2003

NRM – Natural Resources Management

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Summary

Recent research in natural sciences shows that boreal forests' dynamics are much more complex than what many models traditionally used in forestry economics reflect. This essay analyses some challenges of accounting for such complexity. When forest owners continuously harvest several species, more than one harvesting strategy can be optimal. Which one it is depends on the forest's initial state. For some initial states, two different strategies may yield the same welfare. If whole stand harvesting of one tree species is preferred, the optimal period between each harvesting occasions depends on other species' dynamics.

Keywords: Multiple Steady States, Forestry, Non-Convexities, Moose

JEL: Q23, Q26, Q29

This paper has been presented at the "International Conference on Theoretical Topics in Ecological Economics", Trieste, Italy, February 10-12, 2003, a joint initiative of the Abdus Salam International Centre for Theoretical Physics - ICTP, the Beijer International Institute of Ecological Economics, and Fondazione Eni Enrico Mattei – FEEM.

Thanks to my supervisor Karl-Göran Mäler for many discussions about the paper. I also thank Kjell Danell, Karl-Gustaf Löfgren, Eric Nævdal, John Pastor, Hans Wallin, Angels Xabadia (this paper's opponent at the Second World Congress of Environmental and Resource Economists, June 2002, Monterey, CA, US), Göran Ågren, and participants in a seminar given at the department of forestry economics at the Swedish University of Agricultural Sciences in Umeå, January 2002. Thanks to the participants of the Meeting of the Theory group of the Resilience Network, May 3-5, 2000 in Belize (especially William Brock and Simon Levin), who gave me valuable comments on an early draft. I gratefully acknowledge funding from the Swedish Council for Forestry and Agricultural Research (SJFR) and the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (Formas).

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Management challenges for multiple-species boreal forests

1 Introduction

Forestry economics have traditionally represented forest dynamics by using simple growth functions for one species only. The results were usually derived from methods for calculating the optimal rotation period for even-aged forests. These methods were initiated by Faustmann [12], Pressler [36], and Ohlin [30], hereafter called FPO. These models were relevant because during the 20th century, forestry companies in Sweden for example, transformed many forests into highly productive monocultures.

More recently, forests' recreational values have come into focus. Samuelson [38] considered the potential externalities and public services that forests may provide. This implied that the FPO results needed to be altered to account for public interests. Hartman [15] derived a condition to calculate optimal rotation that would include such amenities. Bowes and Krutilla [5] used the optimal control theory to model the choice between timber production and recreation.

Natural scientists have highlighted forests' environmental qualities and warned against biodiversity loss due to clear-cutting and monoculture. Research inspired by Holling [17] and May [26] showed that ecosystem dynamics were complex: not accounting for them would lead to serious surprises. Nonlinearity, interactions between species, disturbances, and threshold effects were some examples of patterns that play a crucial role in ecosystems' dynamics.

For these reasons, economic models of forestry need to account for forests' complex dynamics and multiple uses. A step in that direction is to model forests as sets of several interacting species. Ready et al. [37] studied optimal management of moose and pine in Norway and calculated an optimal rotation period and optimal moose harvest in a model in which there is was feedback between moose and

pine. Modeling recreational and environmental values also requires that species are entered as state variables directly into the objective function to be maximized.

Theories for economic management of resources produced within ecosystems have recently experienced drastic changes due to the model for shallow lakes that Scheffer [39] and Carpenter and Cottingham [8] produced independently of one other. This model accounts for the possibility that such lakes may flip between a clear and a turbid state. Brock and Starrett [7] gave a complete treatment of the problem of optimal management of shallow lakes. They showed that the optimal types of behavior change as functions of key parameters. In the instances when there were multiple-candidate steady states, the existence and location of Skiba points and the resulting sizes of basins of attraction were not obvious. Wagener [46] investigated the presence of Skiba points in one state systems with one co-state control variable and gave a local criterion that ensured the existence of such points in systems with small discount rates. Mäler et al. [25] provided a dynamic economic analysis of shallow lakes managed under common property. Xepapadeas et al. [47] developed an algorithm to solve such a differential game and to explicitly determine the feedback-equilibrium strategies. Perrings and Walker [34] extended this method of modeling to rangelands. In contrast to the previous papers, their models contain several resources that interact with each other.

Extensive literature exists on ecosystem modeling and management where several species interact. In particular, Pastor and others described the complexity of boreal forest ecosystems¹. They pointed out the importance of the interaction of species and non-linearities. Pastor et al. [31] grasped the most important dynamics in boreal forests by using a system of three differential equations that represent the three-species' dynamics.

This paper uses a slightly modified version of that model to analyze the challenges that ecosystem complexity implies when calculating management rules for forestry. In Sweden, there are many small operators, who extensively exploit their forests and continuously harvest small amounts of several species. This paper derives some optimal management rules to guide them. Large companies that exploit their forests more intensively concentrate on large-scale harvesting of coniferous trees. They usually also harvest entire stands at more or less regular time intervals. I

¹See Pastor et al. [32] [33] and Danell et al. [10].

developed rules to calculate the optimal rotation period and conditions under which each harvesting regime is to be preferred. Recent changes in forestry law [43] in Sweden imply that the forest owners must keep some elements of other tree species. As Ready et al. [37] pointed out, moose migrate and are located in different areas during the hunting season than during the winter foraging season, which is the time in which they eat the most pine. This implies that forest owners suffer damage from browsing moose, but they cannot regulate the moose population through hunting because moose are not on their land during the hunting season. So forestry companies seem to have little power to control species other than the ones they harvest. For that reason, the harvesting rules for entire stands of pine derived in this paper account for the presence of other species in the forest.

Optimal management rules for continuous forest harvesting are not very common; this paper makes that contribution to the subject's literature. These rules imply that several equilibria may be optimal. The paper also looks into some consequences of introducing state variables into the objective function to account for recreational values. For entire-stand harvesting, the main contribution is the revision of FPO's results on optimal rotation periods.

Section 2 presents the biological model of a boreal forest and analyzes its dynamic properties. Section 3 models different harvesting regimes. Section 4 presents the computer simulations. Section 5 presents the conclusion.

2 A three-species boreal-forest model

Boreal forests or *taiga* occupy a wide belt around the arctic circle in the northern hemisphere. Boreal tree species are coniferous trees that include spruce and pine and some hardwood species such as aspen and birch. In some countries like Sweden, this type of forest has been largely exploited for cultivation, pasturage, and forestry (Bernes [2]). This paper uses two models for a boreal forest: a very general model and a specific model, which is useful for computer simulations.

2.1 General model

Murray [27] and Gurney and Nisbet [14] presented methods to build and analyze ecosystem models. The very general three-species model (SYS) could represent the

dynamics of boreal forests:

$$\begin{aligned}\dot{x} &= G_x(x, y, z) \\ \dot{y} &= G_y(x, y, z) \\ \dot{z} &= G_z(x, y, z)\end{aligned}\tag{SYS}$$

where x , y , and z represent browsers (moose), caduceus trees (birch), and conifers' (pine) biomasses, respectively. $G_i(x, y, z)$ is the natural growth of species $i \in \{x, y, z\}$ in the absence of harvesting. Such a general model can embed almost any kind of specific dynamics among three species. The variables x , y and z can also be vectors that represent categories within a species or species group. This is useful to model age or space, for example.

Negative biomass values are impossible and impose the restrictions:

$$x \geq 0, y \geq 0 \text{ and } z \geq 0\tag{1}$$

This is equivalent to imposing that $G_i(x, y, z)$ must be non-negative when species i is extinct ($i = 0$). Assume x_0 , y_0 , and z_0 are the initial stock of species at time $t = 0$. If none of the restrictions (1) are binding, and for every $i \in \{x, y, z\}$, $G_i(x, y, z)$ and its derivatives regarding x , y , and z are continuous, then SYS has a unique solution²:

$$\begin{aligned}x(t) &= \varphi_x(x_0, y_0, z_0, t) \\ y(t) &= \varphi_y(x_0, y_0, z_0, t) \\ z(t) &= \varphi_z(x_0, y_0, z_0, t)\end{aligned}\tag{2}$$

In section 3, the SYS model is used to calculate general forestry management rules. Computer simulations require a more precise specification of forests' dynamics. Ideally, one would like to represent forest ecosystems as accurately as possible, including all relevant species, their ages, and spatial distribution. Some simplifications are necessary because such a representation would be rather difficult to work with. This paper focuses on the effects of species' interactions so the model used does not account for age and space.

²See Kuznetsov [22] for more detailed proof.

2.2 Specific model

John Pastor et al. [31] presented a simplified boreal-forest model in which conifers, caduceus trees, and herbivores interacted. A slightly modified version is used here, where pine, birch, and moose are the three interacting species. In Pastor's model, species can move in space. This is not assumed here, and the model represents one homogenous piece of land. Removing the spatial dimension from Pastor's model implies that conifers grow in an uncontrolled way, which is not very realistic. Still, conifers tend to come rather late in the succession of species and are invasive. (Bernes [2]). A convex-concave growth function for conifers is one way to represent such a feature.

Appendix A describes the model and derives a simplified version with calibrated parameters and variables. For $i, j \in \{x, y, z\}$, let r_i be species i 's growth rates with r_x normalized to one and a_{ij} be interaction coefficients of species j on i . Then SYS can be rewritten with growth functions defined by (3). This specific model is called SYS1.

$$\begin{aligned} G_x(x, y, z) &= x - x^2 + a_{xy}xy + a_{xz}xz \\ G_y(x, y, z) &= r_y y - y^2 - a_{yx}xy - a_{yz}z \\ G_z(x, y, z) &= r_z z^2 - z^3 - a_{zx}xz - a_{zy}y \end{aligned} \tag{3}$$

Moose feed on birch and pine, so both tree species have a positive effect on moose biomass, which is proportional to tree stocks ($a_{xy}xy$ and $a_{xz}xz$). The corresponding effect of moose on tree biomass is negative ($-a_{yx}xy$ and $-a_{zx}xz$). The negative term $-x^2$ describes the crowding effect that occurs when the moose population becomes too large. The negative term $-y^2$ describes that birch is shade intolerant. When the density is too high, birch stop multiplying because new plants cannot get enough light. In contrast, pine exhibits a convex-concave growth. When pine biomass is small, young pines establish better with increasing biomass, so growth is convex. When the population becomes larger, competition arises and growth becomes concave. When carrying capacity³ is reached, more pine leads to negative growth. The terms $a_{yz}z$ and $a_{zy}y$ represent the effects of competition between species of trees.

³The carrying capacity for a species is defined here as the population size for which natural growth is equal to zero; when there are no interactions from other species.

Figure 1 shows what a species' growth looks like when species interaction is not

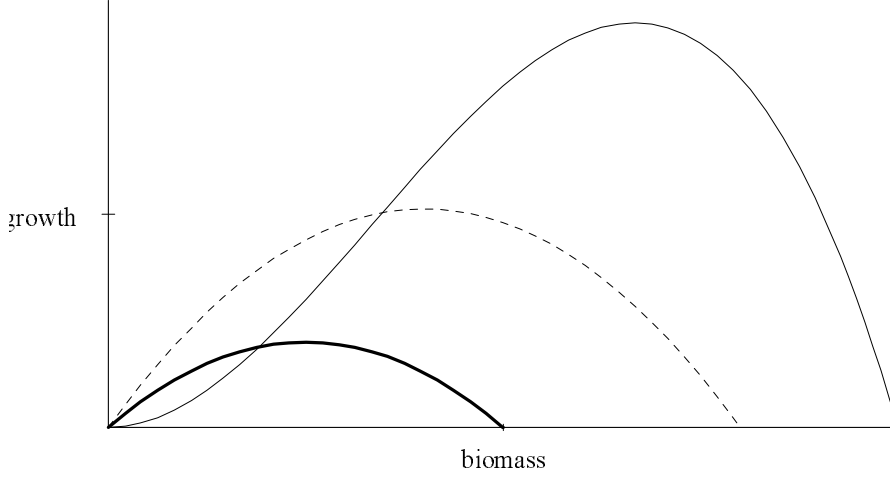


Figure 1: Growth patterns for moose (bold line), birch (dashed line), and pine (thin line)

accounted for. Note that $G_y(x, 0, z)$ and $G_z(x, y, 0)$ are negative so the constraints (1) may be binding for some initial points. Appendix B describes what happens when constraints are binding.

Ecosystem	Steady state	Dynamic properties
extinction	$S0 = (0, 0, 0)$	one unstable or saddle
one species	$S1_x = (1, 0, 0)$	one stable or saddle
	$S1_y = (0, r_y, 0)$	one stable or saddle
	$S1_z = (0, 0, r_z)$	one stable
two species	$S2_\kappa = \left(0, \kappa^2 \frac{r_z - \kappa}{a_{zy}}, \kappa\right)$	one stable, two saddle, one unstable
	$S2_\phi = (1 + a_{xz}\phi, 0, \phi)$	one stable, one saddle
	$S2_g = \left(\frac{1 + a_{xy}r_y}{a_{xy}a_{yx} + 1}, \frac{r_y - a_{yx}}{a_{xy}a_{yx} + 1}, 0\right)$	one stable
three species	$S3_\kappa = (X(\kappa), Y(\kappa), \kappa)$	one stable, three saddle

Table 1: Steady states properties⁴

⁴ κ solves $a_{yz}a_{zy}^2 - r_y r_z a_{zy} Z + r_y a_{zy} Z^2 + Z^3 r_z^2 - 2r_z Z^4 + Z^5$, which has at most four real roots. $\phi = \frac{1}{2} \left(r_z - a_{zx} a_{xz} \pm \sqrt{(r_z - a_{zx} a_{xz})^2 - 4a_{zx}} \right)$. $X(\kappa) = \frac{a_{zy} + a_{xz} a_{zy} \kappa + a_{xy} r_z \kappa^2 - a_{xy} \kappa^3}{a_{zx} a_{xy} \kappa + a_{zy}}$, $Y(\kappa) = \kappa \frac{-a_{zx} + (r_z - a_{zx} a_{xz}) \kappa - \kappa^2}{a_{zy} + a_{xz} a_{zx} \kappa}$.

While a detailed analysis of SYS1's dynamics can also be found in appendix D, the important features are summarized here. Depending on parameter values, SYS1 has up to 15 feasible steady states. Their characteristics are in table 1. Figures 2 and

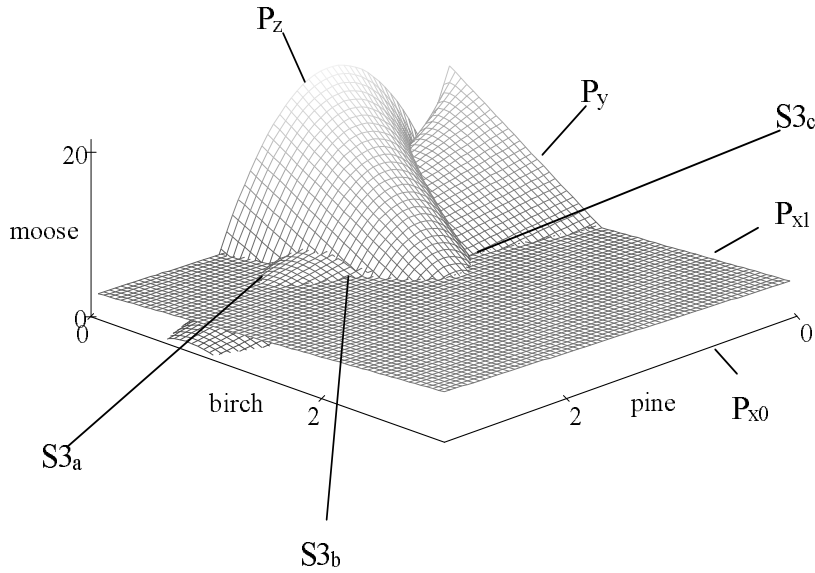


Figure 2: Phase diagram 1

3 show a three-dimensional phase diagram of SYS1, viewed from different angles. Table 2 summarizes the directions of motions in the different regions separated by the manifolds P_{x1} ($\dot{x} = 0, x \neq 0$), P_y ($\dot{y} = 0$), and P_z ($\dot{z} = 0$):

Region	\dot{x}	\dot{y}	\dot{z}
I: below P_{x1}, P_y and P_z	> 0	> 0	> 0
II: below P_{x1}, P_y above P_z	> 0	> 0	< 0
III: below P_{x1}, P_{z1} above P_y	> 0	< 0	> 0
IV: below P_z, P_y above P_{x1}	< 0	> 0	> 0
V: below P_z above P_{x1} and P_y	< 0	< 0	> 0
VI: below P_{x1} above P_z and P_y	> 0	< 0	< 0
VII: below P_y above P_z and P_{x1}	< 0	> 0	< 0
VIII: above P_{x1}, P_y and P_z	< 0	< 0	< 0

Table 2: Directions of motion in different regions

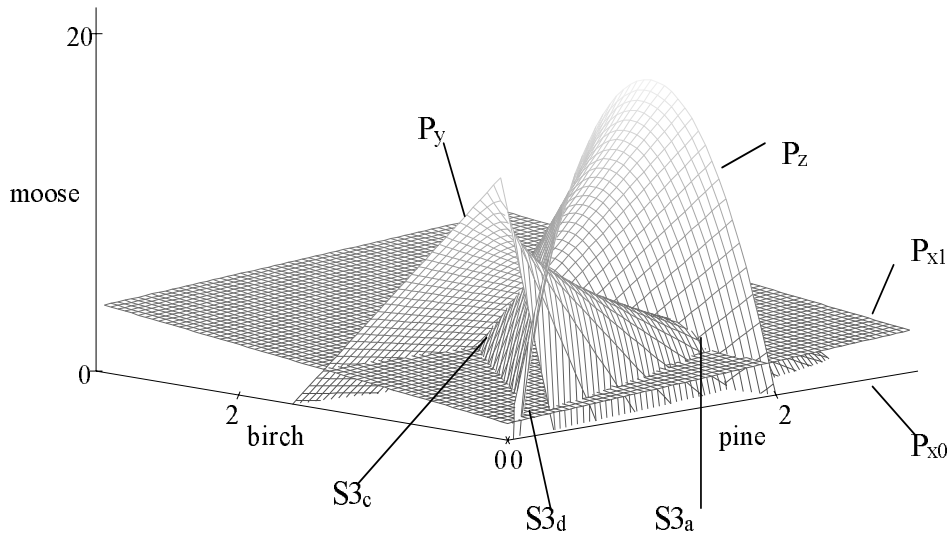


Figure 3: Phase diagram 2

The phase space is also divided into regions so that trajectories that start anywhere in one region will end up in the same stable equilibrium. The manifolds called *separatrices* (Kuznetsov [22]) separate these different regions. The separatrices are difficult to locate in the three-dimensional phase space, but figures 6 and 7 in appendix B show the phase diagram when moose and birch have disappeared, respectively. The dotted curved line shows the separatrices' approximate location in these special cases.

Steady states' simulations with sets of arbitrarily chosen parameters show the fold bifurcations⁵ that might occur. See appendix F. For example, when the birch growth rate varies, six fold bifurcations can be distinguished for values of r_y around 0.5, 0.65, 1.2, 1.45, 1.84, and 1.86. Figures 9-11 in appendix F represent species biomass in a steady state for different birch growth-rate values. They show clearly the fold bifurcations that occur. For low growth rates, no feasible interior steady is stable. Birch cannot maintain itself and becomes extinct. Similar results are

⁵A fold bifurcation is a bifurcation that corresponds to the presence of an eigenvalue equal to zero. When this happens, two equilibria *collide* and disappear. (Kuznetsov [22])

obtained when the other parameters vary.

Computation of the Lyapunov exponents (Lyapunov [24]) for the parameter values tested showed no occurrence of limit cycles or chaos. Nevertheless, Takeuchi [44] studied a slightly different model with two competing preys and one predator and found the existence of a Hopf bifurcation⁶ that lead to periodic orbits. He also found that the three species could coexist in chaotic motion for some parameter values that correspond to a large effect of predation. Takeuchi's results prove that cautiousness is required here. We can only rule out the existence of limit cycles and chaos for the parameter values tested.

These results show that the ecosystem is history dependent: its long-term state depends on the initial state. Furthermore, external shocks that affect the variable stocks or the parameter values may influence the ecosystem's dynamic properties. This may lead to crossing a separatrix so that an external shock can drastically change the ecosystem's long-run equilibrium. Harvesting and hunting are examples of such external shocks. The rest of the paper examines the effects of different exploitation regimes.

3 General management rules for forestry

What happens when harvesting is introduced in ecosystem SYS? Let $h = (h_i)_{i \in \{x,y,z\}}$ be a vector of harvests at time t . To begin with, assume that this vector is arbitrary. The SYS system is transformed into:

$$\begin{aligned}
 \dot{x} &= G_x(x, y, z) - h_x \\
 \dot{y} &= G_y(x, y, z) - h_y \\
 \dot{z} &= G_z(x, y, z) - h_z \\
 x &\geq 0, y \geq 0, z \geq 0
 \end{aligned} \tag{4}$$

It is easy to verify that harvesting affects the separatrices' location and thereby the stable states' basins of attraction. Harvesting may also cause bifurcations; the number of equilibria and their dynamic properties can then differ from the unexploited ecosystem case.

⁶A Hopf bifurcation corresponds to the presence of complex conjugate eigenvalues with zero real parts.

Assume the initial stock of species at time $t = 0$ is x_0 , y_0 , and z_0 . If none of the species becomes extinct, then (4) has a unique solution:

$$\begin{aligned}x(t) &= \Phi_x(x_0, y_0, z_0, t) \\y(t) &= \Phi_y(x_0, y_0, z_0, t) \\z(t) &= \Phi_z(x_0, y_0, z_0, t)\end{aligned}\tag{5}$$

Given that owners harvest forest species to increase their welfare, the next step is to decide what harvesting rules maximize welfare in each period. Section 3.1 derives optimal management rules for owners that continuously harvest several species in the forest. Section 3.2 examines the conditions under which entire-stand harvesting is optimal. The classic FPO result of determining the optimal rotation period is revisited in the case when forestry companies must keep other species (moose and birch) living in the forest for some reasons such as environmental concern.

3.1 Management rules for multiple use

Assume forest owners accounted for the benefits that they can continuously extract from all of the forest's species. To maximize the forest's net benefits, they wanted to find out how much of each species to harvest every time. These benefits were harvesting profits and the forest's net environmental and recreational values.

Let $\Omega_i(h_i)$ represent profits from harvesting species i and $\Omega_e(x, y, z)$ represent net benefits from environmental and recreational services. Functions Ω_i and Ω_e were assumed to be concave. Assume further that the owners gave different positive weights K_x , K_y , K_z and K_e to respective net forest benefits. At time t , the total net benefits were $B(h, x, y, z) = K_x\Omega_x(h_x) + K_y\Omega_y(h_y) + K_z\Omega_z(h_z) + K_e\Omega_e(x, y, z)$. Owners faced the problem:

$$\begin{aligned}\max_h \int_0^{+\infty} B(h, x, y, z) e^{-\rho t} dt \\ \text{s.t. } \dot{x} &= G_x(x, y, z) - h_x \\ \dot{y} &= G_y(x, y, z) - h_y \\ \dot{z} &= G_z(x, y, z) - h_z \\ x &\geq 0, y \geq 0 \text{ and } z \geq 0\end{aligned}\tag{6}$$

Pontryagin et al. [35] developed methods to solve such optimal control problems. This paper uses the method found in Arrow and Kurz [1, Chapter 2] to solve such problems when there are non-negativity constraints on state variables.⁷

Let $h^*(t) = (h_i^*(t))_{i \in \{x,y,z\}}$ represent harvest choices, which are admissible solutions for problem (6). If the constraint qualification (Kuhn and Tucker [20]) was true then there existed functions of time, $\lambda_i(t)$ so that for each t , \mathcal{H} is the current-value Hamiltonian and \mathcal{L} is the Lagrange function:

$$\mathcal{H}(x, y, z, h, \lambda, t) = \sum_i (K_i \Omega_i(h_i) + \lambda_i (G_i(x, y, z) - h_i)) + K_e \Omega_e(x, y, z) \quad (7)$$

$$\mathcal{L}(x, y, z, h, \lambda, \mu, t) = \mathcal{H}(x, y, z, h, \lambda, t) + \sum_i \mu_i (G_i(x, y, z) - h_i) \quad (8)$$

Then $h^*(t)$ maximizes $\mathcal{H}(x, y, z, h, \lambda, t)$ subject to the constraints $G_i(x, y, z) - h_i \geq 0$ for all $i \in \{x, y, z\}$, for which $\dot{h}_i(t) = 0$. Further $\dot{\lambda}_i = \rho \lambda_i - \frac{\partial \mathcal{L}}{\partial \lambda_i}$, evaluated at $i = i(t)$, $h = h^*(t)$, $\lambda = \lambda(t)$. The Lagrange multipliers μ_i must be such that for all i , $\frac{\partial \mathcal{L}}{\partial h_i} = 0$ for $(x, y, z) = (x(t), y(t), z(t))$, $h = h^*(t)$, $\lambda = \lambda(t)$, and $\mu_i(t) i(t) = 0$, $\mu_i(t) (G_i(x, y, z) - h_i) = 0$. The necessary conditions for $h^*(t)$ to be optimal amount to:

- 1) the equations of motion for the exploited ecosystem,

$$\begin{aligned} \dot{x} &= G_x(x, y, z) - h_x \\ \dot{y} &= G_y(x, y, z) - h_y \\ \dot{z} &= G_z(x, y, z) - h_z \end{aligned} \quad (9)$$

- 2) the necessary conditions for optimal harvest, $\forall i \in \{x, y, z\}$,

$$K_i \frac{\partial \Omega_i(h_i^*)}{\partial h_i} - \lambda_i - \mu_i = 0 \text{ or } h_i^* = 0 \quad (10)$$

- 3) the shadow price equations for each species, $\forall i, j \in \{x, y, z\}$,

$$\dot{\lambda}_j = \rho \lambda_j - K_e \frac{\partial \Omega_e(x, y, z)}{\partial j} - \sum_{i \in \{x, y, z\}} (\lambda_i + \mu_i) \frac{\partial G_i(x, y, z)}{\partial j} \quad (11)$$

⁷Hestenes [16] and Seierstad and Sydsæter [41] have developed similar methods.

4) the conditions for the multipliers' non-negativity,

$$\forall i \in \{x, y, z\}, \mu_i(t) i(t) \geq 0, \mu_i(t) (G_i(x, y, z) - h_i) = 0 \quad (12)$$

Conditions (10) are sufficient for optimal harvests because the profits from harvests are additively separable and concave in each harvests, which implies that \mathcal{H} is concave in harvests. Proposition 1 follows directly from equation (10):

Proposition 1 *The optimal size for each species' harvest is such that the marginal value from harvesting more of the species equals the marginal value of retaining more of it in the ecosystem.*

Assume that the equation system (10) has a solution: for $i \in \{x, y, z\}$, the solution is unique because the profit functions are concave and it has the form $h^* = \psi(\lambda)$. So the optimal harvests h_i^* are:

$$h_i^* = \psi_i(\lambda) \text{ or } h_i^* = 0 \quad (13)$$

Conditions (11) imply that in a steady state, for all $j \in \{x, y, z\}$,

$$\rho \lambda_j = K_e \frac{\partial \Omega_e(x, y, z)}{\partial j} + \sum_{i \in \{x, y, z\}} (\lambda_i + \mu_i) \frac{\partial G_i(x, y, z)}{\partial j}$$

Proposition 2 *In a steady state, the interest on a species' marginal value in the ecosystem equals the species' marginal environmental benefit plus the species' marginal benefit in maintaining its own and other species' stock.*

Together, proposition 1 and 2 imply that environmental benefits and other species' stocks must affect harvest size. Whether or not the harvest is higher or lower depends on the species' effects on its own and other species' growth rate, and on the environmental benefits.

If $\widehat{\mathcal{H}}(x, y, z, \lambda, t) \equiv \max_h \mathcal{H}(x, y, z, h, \lambda, t)$, is a concave function of (x, y, z) for given λ and t , then any policy is optimal that satisfies the conditions (9)-(12) and the transversality conditions (14):⁸

$$\lim_{t \rightarrow +\infty} e^{-\rho t} \lambda_i(t) \geq 0, \lim_{t \rightarrow +\infty} e^{-\rho t} \lambda_i(t) i(t) = 0 \quad (14)$$

⁸Arrow and Kurz [1] provide these sufficiency conditions for infinite horizon problems.

Let $\Delta_r(x, y, z)$ be the principal minor of order r in the Hessian for $\widehat{\mathcal{H}}(x, y, z, \lambda, t)$. The maximized Hamiltonian $\widehat{\mathcal{H}}$ is concave on \mathbb{R}_+^3 if and only if for all points (x, y, z) and for all Δ_r , $(-1)^r \Delta_r(x, y, z) \geq 0$ for $r = \{1, 2, 3\}$. In case this condition does not hold, the sufficiency conditions for optimum are not satisfied, and there may be either several, one or no optimal solutions. If there is more than one solution candidate, the comparison of benefits between different solution paths may be necessary to determine, which one is optimal.

When the forest is optimally exploited, two cases can be distinguished and must be analyzed separately.

- Case 1: no species ever becomes extinct.
- Case 2: at least one of the species becomes extinct at some point t_1 in time. This case is a bit complicated because the analysis differs depending on which species disappears first. Appendix I analyzed this case when SYS1 was optimized.

If no species became extinct, the exploited system would follow the equations of motion given by (15):

$$\begin{aligned}
 \dot{x} &= G_x(x, y, z) - \psi_x(\lambda_x) \\
 \dot{y} &= G_y(x, y, z) - \psi_y(\lambda_y) \\
 \dot{z} &= G_z(x, y, z) - \psi_z(\lambda_z) \\
 \dot{\lambda}_x &= \rho\lambda_x - K_e \frac{\partial \Omega_e(x, y, z)}{\partial x} - \sum_{i \in \{x, y, z\}} \lambda_i \frac{\partial G_i(x, y, z)}{\partial x} \\
 \dot{\lambda}_y &= \rho\lambda_y - K_e \frac{\partial \Omega_e(x, y, z)}{\partial y} - \sum_{i \in \{x, y, z\}} \lambda_i \frac{\partial G_i(x, y, z)}{\partial y} \\
 \dot{\lambda}_z &= \rho\lambda_z - K_e \frac{\partial \Omega_e(x, y, z)}{\partial z} - \sum_{i \in \{x, y, z\}} \lambda_i \frac{\partial G_i(x, y, z)}{\partial z}
 \end{aligned} \tag{15}$$

Brock and Malliaris [6] showed methods to study such dynamic systems. Assume the initial species stocks were x_0 , y_0 , and z_0 at $t = 0$ and the initial shadow prices λ_{x_0} , λ_{y_0} , and λ_{z_0} . Then if the system (15)'s right hand side satisfied the Lipschitz condition⁹, it had a unique solution defined by:¹⁰

⁹See Brock and Malliaris [6] for more details.

¹⁰This is the case when $\forall i \in \{x, y, z\}, \psi_i(\lambda_i)$ and its derivatives with regard to λ_i are continuous.

$$\begin{aligned}
x^*(t) &= \Phi_x(x_0, y_0, z_0, \lambda_{x_0}, \lambda_{y_0}, \lambda_{z_0}, t) \\
y^*(t) &= \Phi_y(x_0, y_0, z_0, \lambda_{x_0}, \lambda_{y_0}, \lambda_{z_0}, t) \\
z^*(t) &= \Phi_z(x_0, y_0, z_0, \lambda_{x_0}, \lambda_{y_0}, \lambda_{z_0}, t) \\
\lambda_x^*(t) &= \Phi_{\lambda_x}(x_0, y_0, z_0, \lambda_{x_0}, \lambda_{y_0}, \lambda_{z_0}, t) \\
\lambda_y^*(t) &= \Phi_{\lambda_y}(x_0, y_0, z_0, \lambda_{x_0}, \lambda_{y_0}, \lambda_{z_0}, t) \\
\lambda_z^*(t) &= \Phi_{\lambda_z}(x_0, y_0, z_0, \lambda_{x_0}, \lambda_{y_0}, \lambda_{z_0}, t)
\end{aligned}$$

Assume there is an optimal solution and that the system (15) had at least one steady state.¹¹ Crépin [9] then showed that the eigenvalues of such steady state came in pairs $\alpha, \rho - \alpha$. So the saddle-point properties proven in Kurz [21] remain, even when several steady states existed and the Hamiltonian was not concave. Proposition 3 follows directly:

Proposition 3 *Suppose $\rho > 0$ then, in the neighborhood of a steady state; the system (15) is either totally unstable or has the instability characterized by the saddle-point property.*

If the system has several steady states, then for each of them, there is a limit value for ρ , say $\tilde{\rho}$, under which the steady state exhibits a local saddle-path property or has eigenvalues equal to zero and above which the steady state is locally unstable. This produces a series ($\tilde{\rho}$) of threshold values for ρ . Corollary 4 follows directly.

Corollary 4 *Suppose the system (15) has several steady states. Let $\underline{\rho} = \min(\tilde{\rho})$ and $\bar{\rho} = \max(\tilde{\rho})$. If $\rho < \underline{\rho}$, there is a local saddle path that lead toward each steady state. If $\rho > \bar{\rho}$, all of the steady states are locally unstable. If $\underline{\rho} > \rho > \bar{\rho}$, some steady states are locally unstable while others have a local saddle path.*

Note that often in such problems $\underline{\rho} = 0$ and for $0 < \rho < \bar{\rho}$, there is an odd number of steady states, which come in consecutive pairs of saddle points and unstable states (Birkhoff [4]).

¹¹Unfortunately, the usual existence theorems cannot be applied to guarantee the existence of an optimal solution because the concavity conditions have not necessarily been met. The existence of a steady state of the system (15) is also not guaranteed.

The occurrence of several steady states implies that there is no obvious optimal trajectory from a given starting point. Candidate trajectories toward different equilibria must be compared to determine, which one is optimal. Relation (16) follows from the classic Hamilton-Jacobi result and makes welfare comparisons possible when there is more than one candidate-optimal steady state.

$$\int_0^{+\infty} B(h^*, x, y, z) e^{-\rho t} dt = \frac{1}{\rho} \mathcal{H}(x_0, y_0, z_0, h_0^*, \lambda_0) \quad (16)$$

This relation can also be used to localize Skiba points, which are initial states with more than one optimal path (Beyn et al. [3]). Note that as Deissenberg et al. [11] reminded us, if strict concavity is not given, Skiba points generically do not coincide with the unstable steady states and the latter are not necessarily optimal. Wagener [46] showed that for systems with one state and one control, if there was a cusp bifurcation¹² when the discount rate was zero, then for small positive discount rates, the system had a Skiba point. This result has not yet been generalized to higher dimensions.

All of these results rely on the assumption that it is optimal to continuously harvest all species in the ecosystem. The next section explores conditions when entire-stand harvesting of pine is optimal instead.

3.2 When is entire-stand harvesting optimal?

Assume that forestry companies cannot harvest birch and moose and are not concerned about the forests' environmental and recreational values ($K_e = 0$). When is it an optimal solution to problem (6) to harvest the entire pine stand at given time intervals, assuming $h_x = h_y = 0$ at all points in time? An answer to this question requires that jumps in pine biomass must be allowed. Vind [45] discussed the solution of optimal control problems with jumps in the state variables. This section uses the results given in Seierstad and Sydsæter [41].

Assume interior solutions so $\mu = \mathbf{0}$. Let τ_k be the time when the harvest occurs, where $k \in \mathbb{N}$ is the number of the harvest cycle. Let $z(\tau_k^+)$ and $z(\tau_k^-)$ be the right hand limit and the left hand limit, respectively, of $z(t)$ at τ_k . Forest managers control the harvest's size by choosing a control parameter h_z^k , which represents the

¹²See Kuznetsov [22] for a cusp bifurcation definition.

jump's size. If it is optimal to harvest entire stands of pine at some time τ_k , the magnitude of the jump in pine stock must equal the entire stock before the jump, which is also the harvest size at that time:

$$z(\tau_k^+) - z(\tau_k^-) = -z(\tau_k^-) = -h_z(\tau_k) \equiv -h_z^k$$

The jumps in other species' stocks must equal zero. Between jumps, the forest evolves according to SYS. The reward associated with each jump is the value of the profit from the pine harvest: $K_z \Omega_z(h_z^k)$. Then for $k \in \mathbb{N}$, the necessary conditions for the collection $(x^*, y^*, z^*, h^*, \tau_k^*, \bar{h}_z^k)$, with $h^*(t) = (0, 0, 0)$ for $t \neq \tau_k^*$ and $h^*(\tau_k^*) = (0, 0, \bar{h}_z^k)$ to solve problem (6) are such that:

1. For all non-jump points of the state variables, the necessary conditions derived in section 3.1 (conditions (10) and (11)) must hold with $h^* = (0, 0, 0)$ and $\mu = 0$.
2. At jump points τ_k^* ,

$$\begin{aligned} \lambda_x(\tau_k^{+*}) - \lambda_x(\tau_k^{-*}) &= \lambda_y(\tau_k^{+*}) - \lambda_y(\tau_k^{-*}) = 0 \\ \lambda_z(\tau_k^{+*}) - \lambda_z(\tau_k^{-*}) &= -\frac{K_z \partial \Omega_z(\bar{h}_z^k)}{\partial z} + \lambda_z(\tau_k^{+*}) \frac{\partial z^*(\tau_k^{-*})}{\partial z} \end{aligned}$$

3. and for all possible h_z^k and all $k \in \mathbb{N}$:

$$\underbrace{\left[\frac{K_z \partial \Omega_z(\bar{h}_z^k)}{\partial h_z^k} - \lambda_z(\tau_k^{+*}) \frac{\partial z^*(\tau_k^{-*})}{\partial h_z^k} \right]}_{MV} \times (\bar{h}_z^k - h_z^k) \geq 0$$

4. Moreover, for all h_z^k and for all t at which there is no jump:

$$\left[\frac{K_z \partial \Omega_z(0)}{\partial h_z^k} - \lambda_z(t) \frac{\partial z^*(t)}{\partial h_z^k} \right] \times h_z^k \leq 0$$

Condition 1 may occur when the age of the species to be harvested matters for the value of harvest. If the harvest quality increases with age, it becomes valuable to maintain the species in the ecosystem until the stand is old enough to yield higher

quality. If pine is used as timber, then age greatly matters because young pines produce lower quality timber. If pine is used as fuel, then age may not matter as much. Condition 2 says that the jump in pine shadow price must equal the profit's marginal value when pine biomass changes, plus the value after the jump, of a change in the size of pine stock before harvest due to a change in pine biomass. The jump in other species shadow prices must equal zero. In condition 3, the term MV consists of the marginal change in profits because of a change in harvest's size and of the value of a change in pine stock before harvest because of a change in harvest size. This relation implies that the total value of choosing the optimal size of harvest, must be larger than the total value of choosing any other harvest sizes. Condition 4 says that the total value of any harvest at harvest time that is not optimal must be negative.

3.3 Management rules for entire-stand harvesting

This section presents a problem similar to the FPO optimal rotation problem. The FPO theorem states:

“A forest stand shall be harvested when the rate of change of its value with respect to time is equal to the interest on the value of the stand plus the interest on the value of the forest land.” (Johansson and Löfgren [18, p. 80]).

To simplify the comparison of results, the paper uses a setting similar to Johansson and Löfgren's [18, Chapter 4]. Assume a forestry company exploited pine and that it was optimal to harvest the entire forest at discrete time intervals. Between those harvesting opportunities, nothing is harvested. The FPO result relies on following strong assumptions made here: 1) the capital market is perfect and there is a known interest rate for all future periods; 2) all future timber and input prices are constant and known; 3) the market for forest land is perfect; and 4) the yield of future timber are known. Between harvesting opportunities, the ecosystems follow the motion described by SYS1.

Assume that the forest had been newly harvested and planted at time $T_0 = 0$; at that time, the species' stocks were x_0 , y_0 , and z_0 . Let p_z represent the constant and exogenous net unit price of pine and $h_z(T_k)$ represent pine harvest at time T_k . Let

ρ be the discount rate and C the cost of forestry (planting and harvesting), which is assumed to be independent of harvest timing and size. This rather unrealistic, last assumption was made to simplify comparisons with Johansson and Löfgren. The present profit value from harvesting pine for the first time at time T_1 can be written:

$$\Pi_z (h_z (T_1)) = h_z (T_1) p_z e^{-\rho T_1} - C$$

Between harvests, the forest behaves according to SYS: there is neither thinning nor clearing by assumption. At harvest time, the entire pine stand is harvested and replanted. Let x_{T_k} , y_{T_k} , and z_{T_k} be moose and trees' stocks respectively at harvesting time T_k . These depend on the stocks of species after a previous harvest in the following way:

$$\begin{aligned} x_{T_k} &= \varphi_x (x_{T_{k-1}}, y_{T_{k-1}}, z_{T_{k-1}}, T_k) \\ y_{T_k} &= \varphi_y (x_{T_{k-1}}, y_{T_{k-1}}, z_{T_{k-1}}, T_k) \\ z_{T_k} &= \varphi_z (x_{T_{k-1}}, y_{T_{k-1}}, z_{T_{k-1}}, T_k) \end{aligned}$$

By assumption, it is optimal to harvest entire stands so $h_z (T_1) = z_{T_1}$. The present value of harvesting for the first time at time T_1 is given by:

$$\Pi_z (T_1) = z_{T_1} p_z e^{-\rho T_1} - C$$

The company can decide that $z_{T_1} = z_0$; but unless equation system SYS is periodic of period T_1 , we will typically have $x_{T_1} \neq x_0$ and $y_{T_1} \neq y_0$. This is because the forestry company does not control moose and birch. This implies that the optimization problem at time zero differs from the optimization problem after the completion of the first rotation. After each new rotation period, the forestry company faces a different problem. Proposition 5 follows directly from this observation:

Proposition 5 *If other species affect the harvested tree species' natural growth, the optimal rotation should not usually have the same length in each period.*

Löfgren [23] found a similar result, which showed that genetic or biotechnological progress affected the socially optimal rotation period. The results from Löfgren and this paper indicate that it is restrictive to assume identical rotations, unless the

biomasses of other species are controlled so that they are the same at the start of each period.

The forest land's present value for the forestry company is the sum of the infinite series of all future revenues:

$$V_z = \sum_{k=1}^{+\infty} (\varphi_z(x_{T_{k-1}}, y_{T_{k-1}}, z_{T_{k-1}}, T_k) p_z e^{-\rho(T_k - T_{k-1})} - C) e^{-\rho T_{k-1}}$$

Replacing for φ_z , the first order condition for a maximum forest present value is:

$$\begin{aligned} \frac{\partial V_z}{\partial T_k} &= \frac{\partial z_{T_k}}{\partial T_k} p_z e^{-\rho T_k} - \rho (z_{T_k} p_z - C) e^{-\rho T_k} \\ &+ \left(\frac{\partial z_{T_{k+1}}}{\partial x_{T_k}} \frac{\partial x_{T_k}}{\partial T_k} + \frac{\partial z_{T_{k+1}}}{\partial y_{T_k}} \frac{\partial y_{T_k}}{\partial T_k} + \frac{\partial z_{T_{k+1}}}{\partial z_{T_k}} \frac{\partial z_{T_k}}{\partial T_k} \right) p_z e^{-\rho T_{k+1}} = 0 \end{aligned}$$

This relation transforms into:

$$\underbrace{\frac{\partial z_{T_k}}{\partial T_k} p_z}_A + \underbrace{\left(\frac{\partial z_{T_{k+1}}}{\partial x_{T_k}} \frac{\partial x_{T_k}}{\partial T_k} + \frac{\partial z_{T_{k+1}}}{\partial y_{T_k}} \frac{\partial y_{T_k}}{\partial T_k} + \frac{\partial z_{T_{k+1}}}{\partial z_{T_k}} \frac{\partial z_{T_k}}{\partial T_k} \right) p_z e^{-\rho(T_{k+1} - T_k)}}_B = \rho (z_{T_k} p_z - C) \quad (17)$$

The left-hand side is the marginal net benefit from delaying the harvest at time T_k . The term A represents the value of a marginal change in harvest timing on harvest size at time T_k . B represents the discounted value of the effect of a change in harvest timing on the size of the next harvest, due to changes in each species' stock at the beginning of the new rotation period. The right-hand side is the marginal net cost from not harvesting at time T_k , which consists of the foregone interest on the net benefit from harvesting at time T_k . Hence, proposition 6:

Proposition 6 (Modified FPO) *A forest stand shall be harvested each time the marginal net benefit from delaying the harvest equals the interest on net harvesting benefits at that time.*

One can verify from relation (17) that either a higher timber price or a higher discount rate can lead to earlier harvesting. An increase in price p_z implies that net harvesting benefits increase relatively more than the marginal net benefits from delaying the harvest. Similarly, an increase in discount rate ρ implies that the

marginal net benefits from delaying the harvest decrease, while the marginal net harvesting benefits increase.

The forestry company, which maximizes forestry revenues, must account for other species' effects on future harvests. Changing harvest timing also changes each species' stock level at the start of the next rotation period. This affects harvest potentials at the end of the next rotation period. The interest on forest land value do not enter here; instead, it enters a term that corresponds to the effects of changes in species' stocks.

It is reasonable to assume that the biomass of pine is significantly smaller after harvest and replanting than before. If pine harvesting does not directly affect other species' stocks¹³, it corresponds in figures 2 and 3 to a shift in space parallel to the z -axis. Such a shift may imply that the ecosystem's state crosses a separatrix. If that happens, pine might never recover and become depleted over time. This will occur unless forestry companies plant enough pine.

The pine harvest's effects on moose and birch make the manifolds $\dot{x} = 0$ and $\dot{y} = 0$ shift. The resulting outcome is difficult to forecast: the moose and birch population may either decrease or increase. These effects can be analyzed using the specific SYS1 model. The entire stand is cut at harvesting time and future forest growth is further simulated with a new pine stock, which corresponds to planting. Harvest timing depends on timber price and discount rate.

Figures 4 and 5 show the evolution of the species' biomasses after harvest with the replanting of 0.87 and 0.88 units of pine, respectively. The ecosystem was in a steady state before the harvest. Although the difference in planting is very small, it is essential for future harvesting opportunities. For the smaller planting size, pine cannot recover and the ecosystem ends up in a steady state with no pine. If the harvest occurs before the steady state has been reached so that moose and birch biomasses are higher than in the steady state, the replanting must be larger than 0.88 to maintain the ecosystem's long-term pine biomass. For example, if starting with moose and birch biomasses of 2.835 and 1.007, respectively instead of 2.812 and 0.977 respectively, pine replanting should be a minimum of 0.895.

The effect of not accounting for the dynamics of moose and birch was also checked. Birch and moose were assumed to be fixed at steady-state levels, so forest

¹³For example, this would be the case if other tree species had to be harvested at the same time.

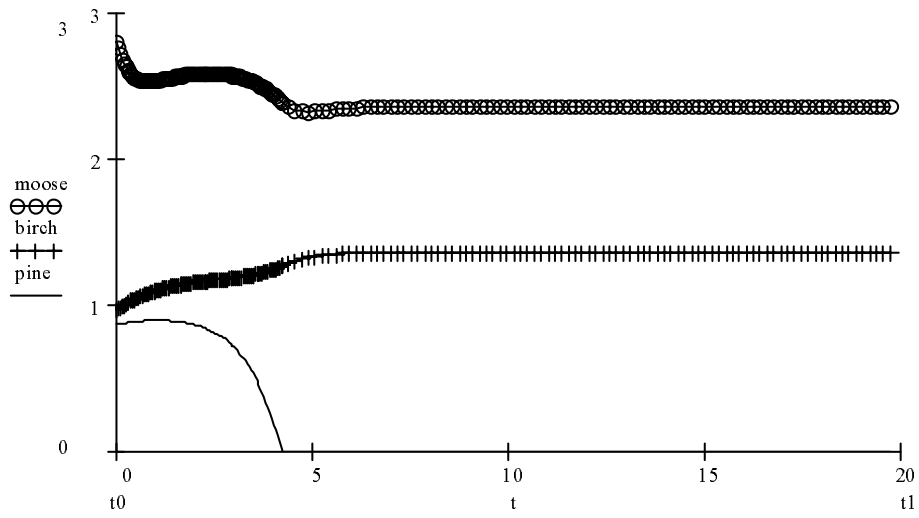


Figure 4: Ecosystem after harvesting when only 0.87 units of pine were planted

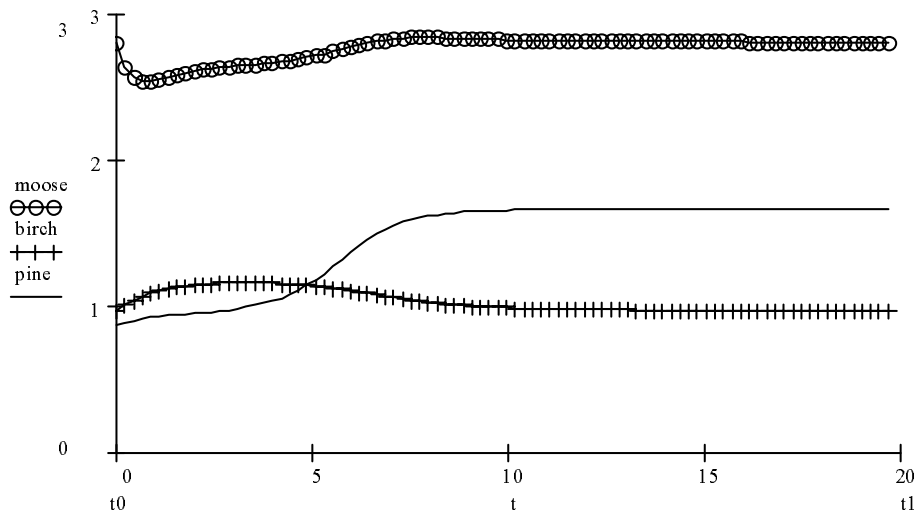


Figure 5: Ecosystem after harvesting when 0.88 units of pine were planted

managers would consider them as constants. This simulation showed that a planting level of 0.83 was enough to maintain pine in the ecosystem. But this planting size is not enough when accounting for other species' dynamics. So forest owners experience a higher risk of depleting their forests if they do not account for other species' dynamics.

Section 4 simulates a specific model of a boreal forest with continuous, multiple-use harvesting.

4 Simulations with a specific model

The simulations aim to answer the following questions: How many steady states exist and are they feasible? What is the optimal path in the exploited forest? What are the dynamics at each steady state? What do the dynamics of the system look like when they are not in a steady state? What is the basin of attraction of the steady states where no species become extinct? What happens in boundary points? Do bifurcations occur when parameters vary?

Kuznetsov [22], Judd [19], and Beyn et al. [3] showed several useful numerical methods. MATHCAD¹⁴ simulated steady states and the dynamics in their neighborhood.¹⁵ Steady state analysis is not enough to obtain a quality picture of the dynamics of the systems of differential equations that have been studied. Each system may have very complex dynamics outside of the steady states. Limit cycles¹⁶ or chaotic attractors¹⁷ may very well be present. Systems' simulations using DYNAMICS¹⁸ (Nusse and Yorke [29]) help picture the systems' dynamics outside steady states. In particular, this program can explore the system for limit cycles and

¹⁴Mathcad is a software used to solve math problem. Both numerical and analytical methods can be used.

¹⁵A copy of this program code can be requested from the author.

¹⁶A limit cycle is an isolated cycle of a continuous time dynamic system. A cycle is a periodic orbit, that is a non-equilibrium orbit such that a trajectory starting at a point will return to the same point after a time period called *period*. See Kuznetsov [22] for a more detailed definition.

¹⁷An attractor is roughly a subset of the phase space toward which the initial conditions may be attracted. An attractor is said to be chaotic when and if we take two typical points on the attractor that are separated from each other by a small distance; then, for increasing time, these points move apart exponentially fast. Thus a small uncertainty in the initial state of the system rapidly leads to the inability to forecast its future. See Grebogi et al [13] for further reading and references on the topic.

¹⁸DYNAMICS is a program that explores the dynamics of differential and difference equation systems.

chaos. MATLAB¹⁹ solved two point boundary value problems and localized Skiba points in the optimized system using the method developed in Beyn et al. [3].

4.1 Multiple-use specific model

Let q_i and c_i be positive constants that represent the unit price and some cost parameters, respectively, for species $i \in \{x, y, z\}$. Let $\alpha_i \equiv K_i c_i$ and $p_i \equiv \frac{q_i}{c_i}$; then a conveniently weighted profit function for harvesting species i is $\pi_i = \alpha_i h_i (p_i - h_i)$. This function has a convex cost part ($\alpha_i h_i^2$) and is concave in harvest.²⁰

Let ζ , η , and θ be constant weights associated with species x, y , and z respectively. $\zeta, \eta, \theta \in (0, 1)$ and $\zeta + \eta + \theta \leq 1$. Environmental and recreational benefits from the forest are then $\Omega_e(x, y, z) = x^\zeta y^\eta z^\theta$. Ω_e is increasing and concave in all species's stocks and the environmental benefits from the forest are zero as soon as one species becomes extinct. This is a strong assumption but the functional form still accounts for important characteristics of environmental and recreational benefits: it increases with number of species and populations sizes.²¹

The multiple-use problem from section 3.1 is now transformed into:

$$\begin{aligned} & \max_h \int_0^{+\infty} \left(\sum_i \alpha_i h_i (p_i - h_i) + K_e x^\zeta y^\eta z^\theta \right) e^{-\rho t} dt \\ \text{st } & \dot{x} = x - x^2 + a_{xy}xy + a_{xz}xz - h_x \\ & \dot{y} = r_y y - y^2 - a_{yx}xy - a_{yz}z - h_y \\ & \dot{z} = r_z z^2 - z^3 - a_{zx}xz - a_{zy}y - h_z \end{aligned}$$

The Lagrange function is still given by (8), and the Hamiltonian (7) is rewritten with appropriate functional forms:

¹⁹MATLAB is a matrix based interactive program doing numeric computation and data visualization.

²⁰This relies on these assumptions: recreational benefits from moose hunting are neglected and profits are assumed to be independent from moose density; timber harvesting has no effect on the timber's market price; and there are no returns to scale.

²¹To measure diversity, alternatives to the Cobb Douglas function can be found in Stirling and Wilsey [42] or Norberg et al. [28].

$$\begin{aligned}
\mathcal{H}(x, y, z, h, \lambda, t) = & \sum_i \alpha_i h_i (p_i - h_i) + K_e x^\zeta y^\eta z^\theta \\
& + \lambda_x (x - x^2 + a_{xy}xy + a_{xz}xz - h_x) \\
& + \lambda_y (r_y y - y^2 - a_{yx}xy - a_{yz}z - h_y) \\
& + \lambda_z (r_z z^2 - z^3 - a_{zx}xz - a_{zy}y - h_z)
\end{aligned}$$

The concavity conditions (18) are complicated. They are computed in appendix G for $K_e = 0$:

$$\begin{aligned}
\lambda_x & \geq 0 \\
4\lambda_x \lambda_y & \geq (\lambda_x a_{xy} - \lambda_y a_{yx})^2 \quad (18) \\
\lambda_z (6z - 2r_z) (4\lambda_x \lambda_y - (\lambda_x a_{xy} - \lambda_y a_{yx})^2) & \geq 2\lambda_y (\lambda_x a_{xz} - \lambda_z a_{zx})^2
\end{aligned}$$

They imply that the marginal value of having moose and birch in the forest, respectively, must be positive. The marginal value of having pine in the forest must be positive if z^* is relatively large ($z^* > \frac{r_z}{3}$), and negative if z^* is relatively small ($z^* < \frac{r_z}{3}$). In each case, z^* must be large enough or small enough to satisfy the third sufficiency condition. When $\frac{r_z}{3}$, the pine population has reached one-third of its carrying capacity. For smaller pine populations, the pines' growth rate is convex. If the pine population is larger, it is concave (recall figure 1).

For $K_e > 0$, that is when recreational and environmental benefits enter the social welfare function, concavity conditions are very tedious to compute. Similarly to when $K_e = 0$, concavity conditions are not always satisfied, which implies that welfare comparisons between trajectories are necessary and the maximizing problem may have one, several or no optimal solutions, depending on the initial state. As pointed out in section 3.1, comparing the value of the Hamiltonian for different initial states can help sort out different optimal trajectory candidates.

The optimal harvest is written, for all i :

$$h_i^* = \frac{1}{2} \left(p_i - \frac{\lambda_i + \mu_i}{\alpha_i} \right), \text{ or } h_i^* = 0$$

When no species are depleted by (12), the Lagrange multipliers must equal zero at

every point in time ($\mu_i = 0$). If shadow prices are large enough compared to costs ($\forall i, p_i > \frac{\lambda_i}{\alpha_i}$), all harvests are positive. Assuming that this is the case, an optimal trajectory $(x^*, y^*, z^*, \lambda^*)$ must solve SYS2.

$$\begin{aligned}
 \dot{x} &= x - x^2 + a_{xy}xy + a_{xz}xz - \frac{1}{2}p_x + \frac{\lambda_x}{2\alpha_x} \\
 \dot{y} &= r_y y - y^2 - a_{yx}xy - a_{yz}z - \frac{1}{2}p_y + \frac{\lambda_y}{2\alpha_y} \\
 \dot{z} &= r_z z^2 - z^3 - a_{zx}xz - a_{zy}y - \frac{1}{2}p_z + \frac{\lambda_z}{2\alpha_z} \\
 \dot{\lambda}_x &= \rho\lambda_x - K_e \zeta x^{\zeta-1} y^\eta z^\theta - \lambda_x (1 - 2x + a_{xy}y + a_{xz}z) + \lambda_y a_{yx}y + \lambda_z a_{zx}z \\
 \dot{\lambda}_y &= \rho\lambda_y - K_e \eta x^\zeta y^{\eta-1} z^\theta - \lambda_x a_{xy}x - \lambda_y (r_y - 2y - a_{yx}x) + \lambda_z a_{zy} \\
 \dot{\lambda}_z &= \rho\lambda_z - K_e \theta x^\zeta y^\eta z^{\theta-1} - \lambda_x a_{xz}x + \lambda_y a_{yz} - \lambda_z (2r_z z - 3z^2 - a_{zx}x)
 \end{aligned} \tag{SYS2}$$

4.2 Simulations

Assessing numerical values to parameters helps simulate this differential equation system. Note that there are some reasons to treat cases $K_e = 0$ and $K_e > 0$ separately. First the system's dynamics are much easier to simulate when $K_e = 0$. Second $K_e = 0$ can also be interpreted as the case of a private owner who only maximizes profits from forestry. Then $\alpha = c_x$, $\beta = c_y$, and $\gamma = c_z$: it is reasonable to believe that private owners do not care about where profits come from, because they have no redistribution goals.

Even when parameters are replaced with numeric values, SYS2's steady states cannot be analytically computed. They must be evaluated numerically, which implies that the number of steady states could be underestimated. Usually, numerically evaluated steady states depend on quality initial guesses; different initial guesses can lead to different steady states. For each set of tested parameter values, the steady states were simulated with MATHCAD using a thousand different randomly chosen initial values between zero and ten for each variable.²²

For the benchmark's parameter values, with $K_e = 0$, SYS2 has four feasible interior steady states ($S3_a^*, S3_b^*, S3_c^*, S3_d^*$) and one steady state with a negative pine biomass, which is not feasible. Three of them ($S3_a^*$, $S3_c^*$ and the infeasible state)

²²Different ranges and different numbers of initial guesses were also tested for some parameter values and did not produce additional steady states.

are saddle points and the other two are unstable with only two eigenvalues with negative real part. This is not surprising given the result stated in proposition 3 and its corollary 4. The existence of a saddle steady state, with negative pine biomass, indicates that for some initial states, depletion of all pine may be optimal. This possibility was studied appendix I.²³ The SYS2 system was simulated to check what happened when pine disappeared. This produced two steady states with no pine. Appendix H shows the variables' values in all steady states. So for the benchmark's parameter values with $K_e = 0$, the optimized forest characterized by SYS2 had at least six feasible steady states, of which at least two lead to pine depletion. It is easy to verify that steady state $S3_c^*$ is the only equilibrium that satisfies the sufficiency conditions 18.

Simulations²⁴ using the method developed in Beyn et al. [3] showed the existence of Skiba points. For example such points were (4.98, 0.5, 1.1), (2, 1.33, 1.1), and (2, 0.5, 1.86). In those points, the welfare obtained by going to steady state $S3_a^*$ was about the same as the welfare obtained when going to $S3_c^*$. This shows that $S3_a^*$ could sometimes be optimal even though the sufficiency conditions do not hold. Whether or not this is true depends on initial conditions.

The sets of all Skiba points form the Skiba manifolds of this system. Locating all Skiba points would be very tedious. According to Beyn et al., the Skiba manifold's dimension should equal the number of state variables, which implied that a Skiba manifold should be of dimension 3.²⁵ To approximate the Skiba manifold, one could use the initial state variables as continuation parameters. Depending on whether or not pine extinction can ever be optimal there might be Skiba manifolds that separate the regions with optimal interior states from the regions where a steady state with no pine is optimal.

The effects of variations in the birch growth rate on respective species' biomasses in steady states were simulated in the case when environmental benefits were not accounted for ($K_e = 0$). These simulations also showed bifurcations for low birch growth rates. For r_y below 0.45, there was only one feasible steady state; for r_y above 0.65, there were four and in between, there were three steady states.

²³Note that the general saddle point property stated in proposition 3 does not remain when some species are extinct.

²⁴The program codes can be requested from the author.

²⁵Except if there are more than two optimal trajectories from a Skiba point or if the stable manifold's dimension differs from the number of state variables.

When a social planner accounted for environmental benefits, the results were modified. Some simulations showed that the number of steady states was generally higher for relatively low birch growth rates and smaller for higher birch growth rates. Comparing the steady states in both management regimes shows that the saddle points have higher levels of each population when environmental benefits are accounted for. This is not true for the unstable equilibria, which are probably not optimal but this is not proved yet. For the benchmark's parameter values, there are only three steady states and no infeasible saddle point. This hints that the risk of pine becoming extinct is much lower when environmental benefits are accounted for, which is not surprising.

5 Concluding remarks

The existence of one or more Skiba manifolds reveals the exploited ecosystem's dependency on history. What is optimal for one state of the world is not necessarily optimal for another. This has consequences for how to regulate the system. If an optimal trajectory passes close to a Skiba manifold, small mistakes in the regulation may lead to the manifold's crossing, in which case the opportunities of future harvests and their consequences on the ecosystem can be completely modified. Exogenous changes in the system can also lead to a Skiba manifold crossing. Such exogenous changes include any changes that affect the variables, such as diseases, storms, and exogenous market shocks.

Multiple species and non-concave growth functions lead to multiple optimal states and Skiba points, so margin analysis is usually not enough to determine the optimal trajectory at given initial points. One must know all future harvesting benefits to find out which trajectory is optimal.

Under conditions determined in section 3.2, it is optimal to harvest entire pine stands at once. These conditions may occur when age influences profits derived from the harvest. This is the case, for example, when pine is harvested to be used as timber or when there are extra profits to be made if harvesting can be concentrated on a specific point in time.

FPO's classic result on an optimal rotation period in that situation must be revisited to support the presence of other species. If forestry companies do not account for other species' effect, then they face a higher risk of depleting pine because

they tend to replant fewer trees than necessary. Even if they were to account for other species' dynamics, they need to plant more after harvesting if the harvesting time occurs before the ecosystem is able to recover and reach its steady state. In real life, the forestry companies do not know the dynamics of the forests. Under these conditions, following optimal harvest rules for only one species is risky because these rules may induce a more intensive exploitation than what the forest can sustain. Of course, accounting for other species does not solve the problem because some species and large parts of the forests' dynamics are still unknown. But this could help forest managers become more conscious about the needs for alternative harvesting rules. In particular, there is a need for future research to determine the approximate magnitude of mistakes due to the use of wrong models to represent ecosystem production.

A Dimensionless ecosystem model

Let S_1 , S_2 and S_3 represent the stocks of moose, birch and pine biomasses, respectively, at time t . Let r_1 , r_2 and r_3 represent the corresponding growth rates; $a_{i,j}$ represent the effects of species j on i for each two-way interaction. The following differential equations system represents the evolution in time of respective biomass density.

$$\begin{aligned}\frac{\partial S_1}{\partial t} &= r_1 S_1 (1 - a_{11} S_1) + a_{12} S_1 S_2 + a_{13} S_1 S_3 \\ \frac{\partial S_2}{\partial t} &= r_2 S_2 (1 - a_{22} S_2) - a_{21} S_1 S_2 - a_{23} S_3 \\ \frac{\partial S_3}{\partial t} &= r_3 S_3^2 (1 - a_{33} S_3) - a_{31} S_1 S_3 - a_{32} S_2\end{aligned}$$

Following Segel [40], I rewrite the system in dimensionless form. Let suffix u denote the unit used to measure respective variables' size. Let $x \equiv \frac{S_1}{S_{1u}}$, $y \equiv \frac{S_2}{S_{2u}}$, $z \equiv \frac{S_3}{S_{3u}}$ and $\tau \equiv \frac{t}{t_u}$. This yields:

$$\begin{aligned}\dot{x} &= \frac{\partial x}{\partial \tau} = \frac{\partial \left(\frac{S_1}{S_{1u}} \right)}{\partial t} \frac{dt}{d\tau} = t_u (r_1 x (1 - a_{11} S_{1u} x) + a_{12} x S_{2u} y + a_{13} x S_{3u} z) \\ \dot{y} &= \frac{\partial y}{\partial \tau} = \frac{\partial \left(\frac{S_2}{S_{2u}} \right)}{\partial t} \frac{dt}{d\tau} = t_u \left(r_2 y (1 - a_{22} S_{2u} y) - a_{21} S_{1u} x y - \frac{a_{23} S_{3u}}{S_{2u}} z \right)\end{aligned}$$

$$\dot{z} = \frac{\partial z}{\partial \tau} = \frac{\partial \left(\frac{S_3}{S_{3u}} \right)}{\partial t} \frac{dt}{d\tau} = t_u \left(S_{3u} r_3 z^2 (1 - a_{33} S_{3u} z) - a_{31} S_{1u} x z - \frac{a_{32} S_{2u}}{S_{3u}} y \right)$$

Let $t_u \equiv \frac{1}{r_1}$, $S_{1u} \equiv \frac{1}{a_{11}}$, $S_{2u} \equiv \frac{r_1}{r_2 a_{22}}$ and $S_{3u} \equiv \sqrt{\frac{r_1}{r_3 a_{33}}}$, the system becomes:

$$\begin{aligned} \dot{x} &= x - x^2 + \frac{a_{12}}{r_2 a_{22}} xy + \frac{a_{13}}{\sqrt{r_1 r_3 a_{33}}} xz \\ \dot{y} &= \frac{r_2}{r_1} y - y^2 - \frac{a_{21}}{r_1 a_{11}} xy - \frac{a_{23} a_{22} r_2}{r_1 \sqrt{r_1 r_3 a_{33}}} z \\ \dot{z} &= \sqrt{\frac{r_3}{r_1 a_{33}}} z^2 - z^3 - \frac{a_{31}}{r_1 a_{11}} xz - \frac{a_{32} \sqrt{r_1 r_3 a_{33}}}{r_1 r_2 a_{22}} y \end{aligned}$$

Finally put $\frac{a_{12}}{r_2 a_{22}} \equiv a_{xy}$, $\frac{a_{13}}{\sqrt{r_1 r_3 a_{33}}} \equiv a_{xz}$, $\frac{r_2}{r_1} \equiv r_y$, $\frac{a_{21}}{r_1 a_{11}} \equiv a_{yx}$, $\frac{a_{23} a_{22} r_2}{r_1 \sqrt{r_1 r_3 a_{33}}} \equiv a_{yz}$, $\sqrt{\frac{r_3}{r_1 a_{33}}} \equiv r_z$, $\frac{a_{31}}{r_1 a_{11}} \equiv a_{zx}$, $\frac{a_{32} \sqrt{r_1 r_3 a_{33}}}{r_1 r_2 a_{22}} \equiv a_{zy}$ to obtain the dimensionless SYS1 ecosystem.

$$\begin{aligned} \dot{x} &= x - x^2 + a_{xy} xy + a_{xz} xz \\ \dot{y} &= r_y y - y^2 - a_{yx} xy - a_{yz} z \\ \dot{z} &= r_z z^2 - z^3 - a_{zx} xz - a_{zy} y \end{aligned} \tag{SYS1}$$

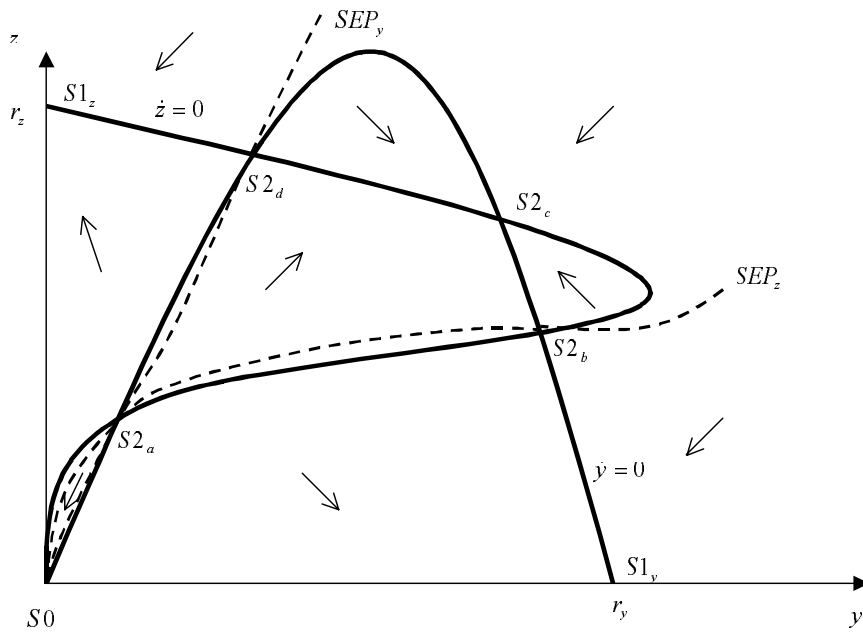
B Boundary analysis

If one or more variables reach the lower bound that restrictions (1) impose, then after that point (t_1) in time, (2) is not necessarily the solution of SYS1.

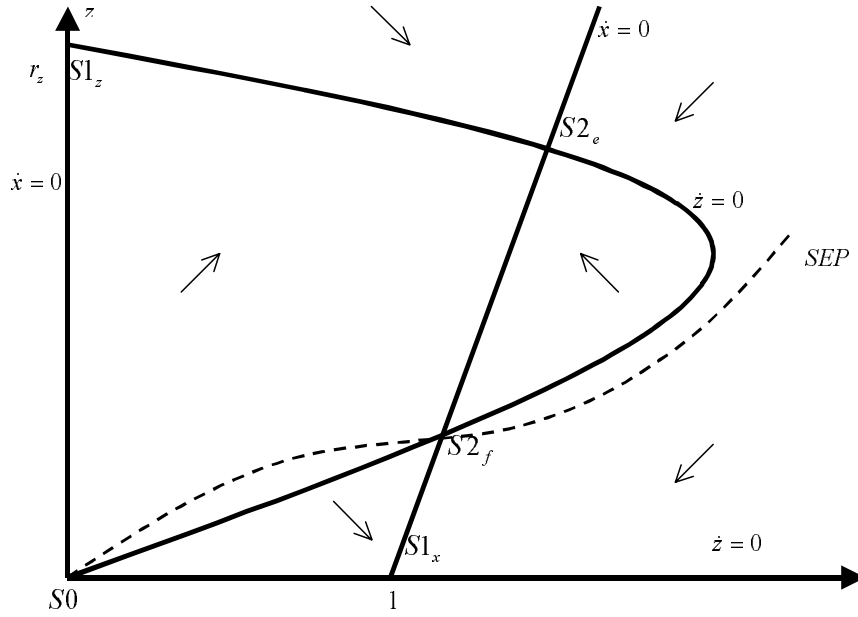
- Suppose $x = 0$; $\dot{x} = 0$, at $t = t_1$, so moose remain extinct and the forest hosts only trees. For $t \geq t_1$, equations 19 characterize the forest's dynamics:

$$\begin{aligned} \dot{y} &= r_y y - y^2 - a_{yz} z \\ \dot{z} &= r_z z^2 - z^3 - a_{zy} y \end{aligned} \tag{19}$$

This forest's steady states are the same as SYS1's steady states when $x = 0$. So even after t_1 , equations (2) still solve SYS1. The steady states are of the form $S_0 = (0, 0, 0)$ and $S_{2\kappa} = \left(0, \kappa^2 \frac{r_z - \kappa}{a_{zy}}, \kappa \right)$ and κ solves $a_{yz} a_{zy}^2 - r_y r_z a_{zy} \kappa + r_y a_{zy} \kappa^2 + \kappa^3 r_z^2 - 2r_z \kappa^4 + \kappa^5 = 0$. The coefficients in the right

Figure 6: Phase diagram when $x = 0$

hand side change sign four times, so following Descartes' rule, there are at most four positive real solutions. Figure 6 shows the system's phase diagram if five steady states are feasible: $S2_c$ is the only stable interior state; $S2_{b,d}$ are saddle points; and $S2_a$ is unstable. There are two other stable states, $S1_y = (0, r_y, 0)$ and $S1_z = (0, 0, r_z)$, which are not stable states of (19). They occur if pine and birch, respectively, disappear after moose became extinct. The separatrices (Kuznetsov [22]) separate the stable states' basins of attraction. They are called SEP_y and SEP_z and their approximate location is given in dotted curved lines. For initial points below SEP_z , pine disappear and the forest reaches the $S1_y$ stable state or $S0$. For initial points above SEP_y , birch is depleted and the forest reaches the $S1_z$ stable state or $S0$. An initial point between the two curves and above $S2_a$ has an optimal trajectory toward $S2_c$. If the initial point is between both curves but below $S2_a$, the optimal trajectory goes toward $S0$. The separatrices intersect at $S2_a$ and $S0$. Comparing $\frac{dz}{dy}$ and $\frac{\dot{z}}{\dot{y}}$ in the neighborhood of $\dot{y} = 0$ and $\dot{z} = 0$, respectively, helps determine the separatrices' approximate location compared to the $\dot{y} = 0$ and $\dot{z} = 0$ curves, respectively.


 Figure 7: Phase diagram when $y = 0$

- Suppose $y = 0$ at $t = t_1$. Birch is extinct so from time t_1 , equations 20, combined with $y = 0$, characterize the forest:

$$\begin{aligned}\dot{x} &= x - x^2 + a_{xz}xz \\ \dot{z} &= r_z z^2 - z^3 - a_{zx}xz\end{aligned}\tag{20}$$

There are at most five feasible steady states: S_0 , $S_{1x} = (1, 0, 0)$, S_{1z} , and $S_{2e,f} = (1 + a_{xz}\nu, 0, \nu)$, in which $\nu = \frac{1}{2} \left(r_z - a_{zx}a_{xz} \pm \sqrt{(r_z - a_{zx}a_{xz})^2 - 4a_{zx}} \right)$. The steady states $S_{2e,f}$ are only feasible if $r_z > a_{zx}a_{xz} + 2\sqrt{a_{zx}}$. In other words, a steady state with positive moose and pine population exists if and only if pine's natural growth rate is large enough compared to browsing effects on moose and pine growth. Figure 7 shows this system's phase diagram when $S_{2e,f}$ are feasible. When five steady states are feasible, S_{1x} and S_{2e} are stable and the other states are saddle points. Steady states $S_{2e,f}$ are not steady states of SYS1. S_{2f} and S_0 help determining the location of the separatrix SEP , which separates trajectories going toward S_{2e} from trajectories going toward S_{1x} . The dotted curve in

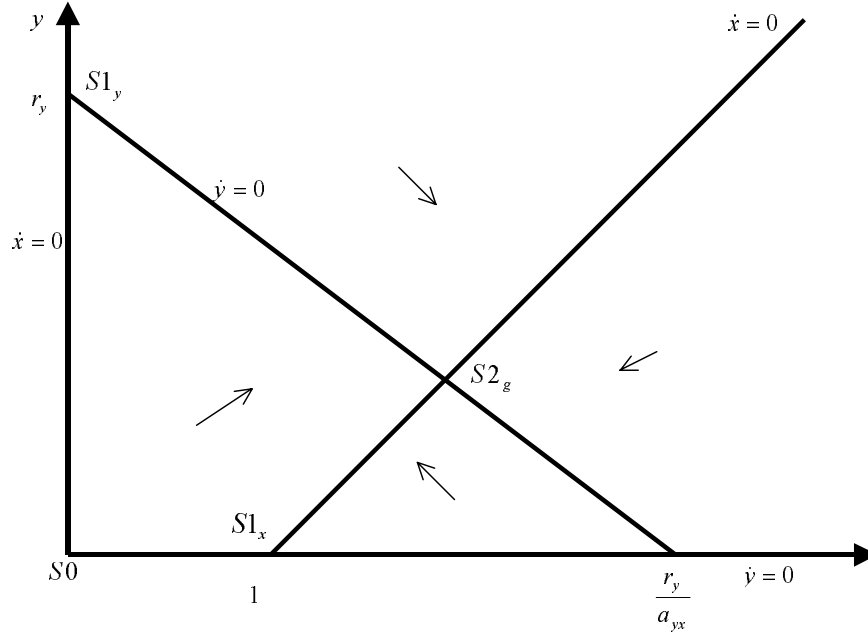
Figure 8: Phase diagram when $z = 0$

figure 7 represents the approximate location of the separatrix. Comparison of $\frac{dz}{dx}$ and $\frac{\dot{z}}{z}$ in the neighborhood of $\dot{z} = 0$ helps determining the approximate location of the separatrix compared to the $\dot{z} = 0$ curve.

- Finally if $z = 0$ at $t = t_1$, pine is extinct so for $t \geq t_1$, equations 21 characterize the forest:

$$\begin{aligned}\dot{x} &= x - x^2 + a_{xy}xy \\ \dot{y} &= r_y y - y^2 - a_{yx}xy\end{aligned}\tag{21}$$

If $z = 0$, the forest has at most four feasible steady states: $S0$, $S1_x$, $S1_y$ and $S2_g = \left(\frac{1+a_{xy}r_y}{a_{xy}a_{yx}+1}, \frac{r_y-a_{yx}}{a_{xy}a_{yx}+1}, 0 \right)$. $S2_g$ exists only if $\frac{r_y}{a_{yx}} > 1$; in other words, if the growth rate of birch divided by the browsing effect is larger than the growth rate of moose. Birch becomes extinct otherwise. This steady state is not a steady state of SYS1. In the (x, y) plane, $S0$ is unstable; $S1_x$ and $S1_y$ are saddle point, if $S2_g$ exists, otherwise $S1_x$ is stable; and $S2_g$ is a stable state if and only if $r_y > \frac{a_{yx}-1}{1+a_{xy}}$. $S2_g$ cannot be the center of a limit cycle; it can only be a stable node or a stable focus. Figure 8 shows this system's phase diagram

when $S2_g$ is feasible and stable. All trajectories starting in the interior of the plane end up in this stable state.

C Steady state analysis

MAPLE solved the steady states for SYS1: $S0 = (0, 0, 0)$, $S1 = (1, 0, 0)$, $S2_\chi = (0, \chi^2 \frac{r_z - \chi}{a_{zy}}, \chi)$, and $S3_\chi = \left(\frac{1a_{zy} + a_{xz}a_{zy}\chi + a_{xy}r_z\chi^2 - a_{xy}\chi^3}{a_{zx}a_{xy}\chi + a_{zy}}, \chi \frac{-1a_{zx} + (r_z - a_{zx}a_{xz})\chi - \chi^2}{a_{zy} + a_{xz}a_{zx}\chi}, \chi \right)$. The variable χ is a root of $AZ^5 + BZ^4 + CZ^3 + DZ^2 + EZ + F$, and

$$A = 1 + a_{yx}a_{xy}$$

$$B = -2(r_z + (a_{yx}a_{xy})^2) + (a_{yx}a_{xy} + 2)a_{xz}a_{zx}$$

$$C = (a_{yx}a_{xy} + 1)r_z^2 + ((a_{yx} + r_y)a_{xy} + 2)a_{zx} + (a_{zx}a_{xz})^2 - a_{xz}(a_{yx}(a_{zy} + a_{xy}r_z a_{zx}) + 2r_z a_{zx})$$

$$D = r_y a_{zy} + a_{zx}^2 a_{xz} \left(2 + a_{xy} r_y + \frac{a_{yz} a_{xy}^2}{a_{xz}} \right) + a_{yx} a_{xz} a_{zy} r_z - a_{yx} a_{zy} (1 + a_{xz}^2 a_{zx}) - a_{zx} r_z (a_{xy} (r_y + a_{yx}) + 2)$$

$$E = -r_y r_z a_{zy} - 2a_{yx} a_{zy} a_{zx} a_{xz} + 2a_{zy} (a_{zx} a_{yz} a_{xy} + a_{yx} r_z) + a_{zx}^2 \left(1 + a_{xy} r_y + \frac{r_y a_{zy} a_{xz}}{a_{zx}} \right)$$

$$F = a_{yz} a_{zy}^2 + r_y a_{zy} a_{zx} - a_{yx} a_{zy} a_{zx}$$

This is a fifth order polynomial and the fundamental theorem of algebra applies, so there are at most five distinct roots real or complex. Unfortunately, Descartes rule is difficult to apply here because the signs of B , C , D , E and F depend on parameter values. But there is at least one real root. This means that the equation system can have at least four and at most twelve different equilibria.

D Dynamic analysis

Appendix C proves that SYS1 has at least four different steady states and at most twelve if there are no restrictions on variables. If non-negativity restrictions apply, one or more of these steady states might not be feasible because of complex or negative variable value. In this last case there are five boundary states: $S1_{y,z}$ and $S2_{e,f,g}$ (see section B). For the parameter values in appendix E, the system has fifteen feasible steady states, including boundary states:

$$S0, S1_{x,y,z}, S2_\kappa = \left(0, \kappa^2 \frac{r_z - \kappa}{a_{zy}}, \kappa \right), S2_{e,f,g}, \text{ and}$$

$$S3_\kappa = \left(\frac{a_{zy} + a_{xz}a_{zy}\kappa + a_{xy}r_z\kappa^2 - a_{xy}\kappa^3}{a_{zx}a_{xy}\kappa + a_{zy}}, \kappa \frac{-a_{zx} + (r_z - a_{zx}a_{xz})\kappa - \kappa^2}{a_{zy} + a_{xz}a_{zx}\kappa}, \kappa \right). \text{ The variable } \kappa \text{ is a root}$$

of a fifth-degree polynomial. κ has at most five different real values of which one is negative, and hence rules out two candidate steady states. The dynamics around the interior states is analyzed graphically.

Construction of a three-dimensional phase diagram requires to represent the manifolds corresponding to $\dot{x} = 0$, $\dot{y} = 0$, and $\dot{z} = 0$. They divide \mathbb{R}_+^3 into different regions in which the system's dynamics are calculated. For the parameter values used in the phase diagram (See figures 2 and 3), there are four interior steady states, $S3_a$, $S3_b$, $S3_c$, and $S3_d$.

- The planes P_{x0} ($x = 0$) (which gives boundary solutions) and P_{x1} ($x = 1 + a_{xy}y + a_{xz}z$) represent equation $\dot{x} = 0$ in \mathbb{R}_+^3 . For points situated below P_{x1} , moose density x increases, whereas it decreases for points above P_{x1} . The location of P_{x1} depends on the growth rate of moose, and on the interaction coefficients of pine and birch on moose. P_{x1} intersects with the y -axis in $y = \frac{-1}{a_{xy}}$ and with the z -axis in $z = -\frac{1}{a_{xz}}$. The intersection of P_{x1} with the plane (y, z) is a straight line with equation $y = \frac{-a_{xz}z - 1}{a_{xy}}$. So an increase in the growth rate of moose causes a shift toward more moose. An increase in the interaction coefficient of birch on moose causes an upward tilt (the negative slope becomes larger in the y -direction). An increase in the interaction coefficient of pine on moose causes an upward tilt in z -direction.
- The manifold P_y ($x = \frac{r_y - y^2 - a_{yz}z}{a_{yx}y}$) represents $\dot{y} = 0$ in \mathbb{R}_+^3 . Birch density increases below P_y and decreases above P_y . The location of the P_y -manifold depends on birch growth rate and the interaction coefficients of moose and pine, respectively, on birch. The P_y -manifold intersections with the (x, y) plane correspond to two straight lines: the x -axis and $y = r_y - xa_{yx}$. The lines intersect in point $(\frac{r_y}{a_{yx}}, 0)$. The intersection with the (y, z) plane is a parabola with equation $z = y\frac{r_y - y}{a_{yz}}$ and maximum $(y = \frac{r_y}{2}, z = \frac{(r_y)^2}{4a_{yz}})$ that intersects with the y -axis in 0 and r_y . An increase in the growth rate of birch causes an upward shift of the manifold. An increase in the interaction coefficient of moose on birch causes a tilt upward in z -direction (the "tail" is shorter). An increase in the interaction coefficient of pine on birch makes the manifold flatter.
- The manifold P_z ($x = \frac{r_z z^2 - z^3 - a_{zy}y}{a_{zx}z}$) represents $\dot{z} = 0$ in \mathbb{R}_+^3 . Pine density z increases below P_z and decreases above. The location of the P_z manifold

depends on the growth rate of pine and on the interaction coefficients of moose and birch on pine. The intersection of P_z with plane (x, z) is a parabola. The intersection with plane (y, z) is a convex-concave curve with equation $y = \frac{r_z z^2 - z^3}{a_{zy}}$. The intersection with plane (x, y) is the point S_0 . An increase in pine growth rate increases the curvature of P_z giving a steeper manifold with a higher maximum. An increase in the interaction coefficient of birch on pine makes P_z steeper and more decreasing in y direction, the tail becomes shorter. An increase in the interaction coefficient of pine on moose makes the manifold flatter in x direction.

These four manifolds define at most eight regions in which the directions of motion are known. These regions are summarized in table 2 in section 2.2. Similarly to the two-dimensional systems studied in section B, there are separatrices between the basins of attraction of the stables equilibria. Unfortunately they are not easy to represent graphically.

Each parameter affects the location and the dynamics around at least one manifold, so each such variation can produce a bifurcation. The fold bifurcation is this model's most common bifurcation but other types of bifurcations might also be encountered. Steady states S_0 and S_1 are present in the model, no matter parameter values.

E Parameter values in the benchmark

parameter	r_y	r_z	a_{xy}	a_{xz}	a_{yx}	a_{yz}	a_{zx}	a_{zy}	ρ	α
value	1.6	2	1	0.5	0.1	0.2	0.05	0.7	0.02	1
parameter	β	γ	K_e	q_x	q_y	q_z	ζ	η	θ	
value	1	1	0.1	1	2	2	1/3	1/3	1/3	

F Simulations

SYS1's steady states were simulated with enough sets of arbitrary chosen parameters. These simulations showed some fold bifurcations. Figures 9-11 show steady state species stocks when birch growth rate varies. Similar bifurcations existed when other parameters were varied.

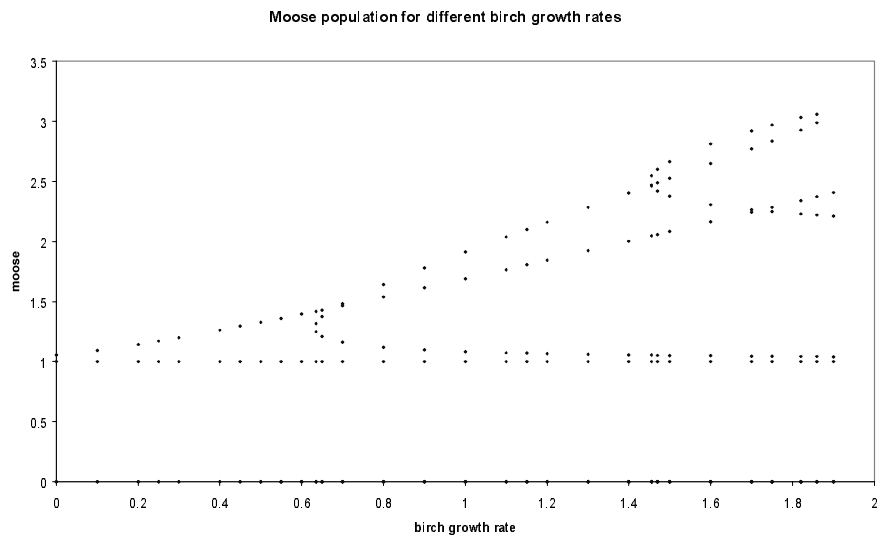


Figure 9: Fold bifurcations (moose)

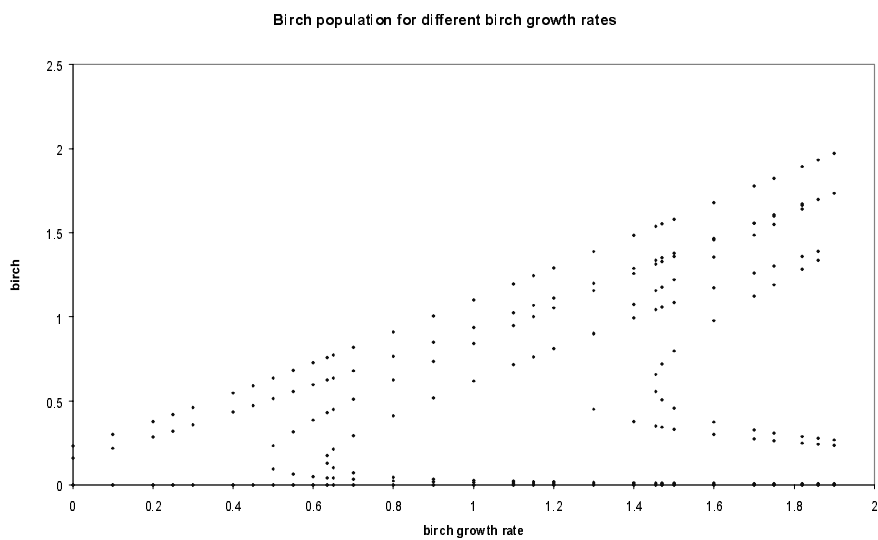


Figure 10: Fold bifurcations (birch)

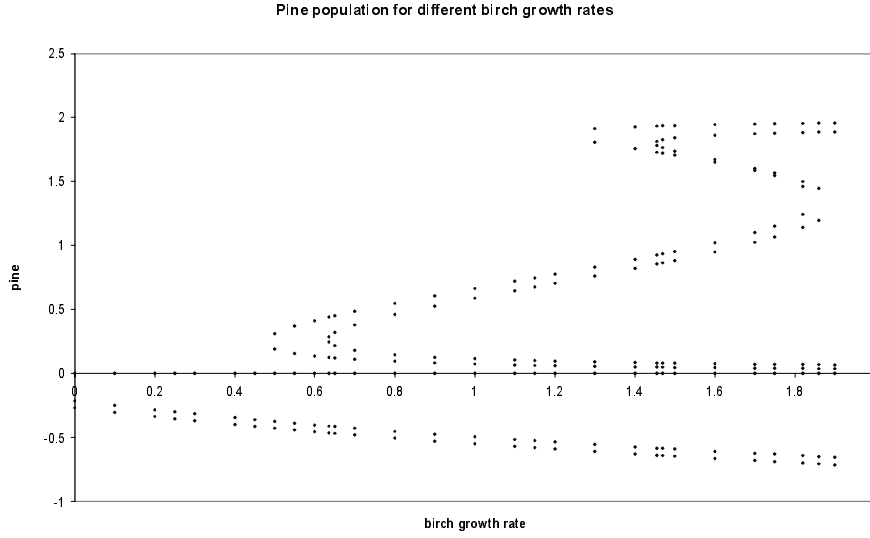


Figure 11: Fold bifurcations (pine)

G Concavity condition

Let $\Delta_r(x, y, z)$ be the principal minor of order r in the Hessian for $\hat{\mathcal{H}}(x, y, z, \lambda, t)$. The maximized Hamiltonian $\hat{\mathcal{H}}$ is concave on \mathbb{R}_+^3 if and only if for all points (x, y, z) and for all Δ_r , $(-1)^r \Delta_r(x, y, z) \geq 0$ for $r = 1, 2, 3$. The Hessian for $\hat{\mathcal{H}}(x, y, z, \lambda, t)$ is given by:

$$\begin{bmatrix} -2\lambda_x & \lambda_x a_{xy} - \lambda_y a_{yx} & \lambda_x a_{xz} - \lambda_z a_{zx} \\ \lambda_x a_{xy} - \lambda_y a_{yx} & -2\lambda_y & 0 \\ \lambda_x a_{xz} - \lambda_z a_{zx} & 0 & \lambda_z (2r_z - 6z) \end{bmatrix}$$

From this, it follows that:

$$\begin{aligned} (-1)^1 \Delta_1(x, y, z) &= 2\lambda_x \\ (-1)^2 \Delta_2(x, y, z) &= 4\lambda_x \lambda_y - (\lambda_x a_{xy} - \lambda_y a_{yx})^2 \\ (-1)^3 \Delta_3(x, y, z) &= 4\lambda_x \lambda_y \lambda_z (2r_z - 6z) - (\lambda_x a_{xy} - \lambda_y a_{yx})^2 \lambda_z (2r_z - 6z) \\ &\quad + 2\lambda_y (\lambda_x a_{xz} - \lambda_z a_{zx})^2 \end{aligned}$$

This yields the concavity conditions:

$$\lambda_x \geq 0$$

$$4\lambda_x\lambda_y \geq (\lambda_x a_{xy} - \lambda_y a_{yx})^2$$

$$\lambda_z (6z - 2r_z) (4\lambda_x\lambda_y - (\lambda_x a_{xy} - \lambda_y a_{yx})^2) \geq 2\lambda_y (\lambda_x a_{xz} - \lambda_z a_{zx})^2$$

H Steady states when harvesting is continuous

The steady states in bold are saddle points.

Steady state	x	y	z	λ_x	λ_y	λ_z
S3_a*	1.767	0.503	1.138	-0.078	1.53	0.672
S3 _b *	0.979	0.367	0.971	-0.71	1.555	0.668
S3_c*	0.234	0.624	1.207	0.067	1.294	0.591
S3 _d *	0.537	0.231	0.036	0.235	1.407	2.32
S2 _a *	2.14	2.837	0	-6.263	10.233	2
S2 _b *	2.263	1.525	0	-0.186	2.46	2

I Extinction in controlled ecosystems

Seierstad and Sydsæter [41] developed methods to analyze what happens when conditions on state variables became binding. Denote by k the species that disappeared at time T . The multipliers were equal to zero ($\mu_i = 0$) before time T occurred. It is reasonable to assume that $h_k^* = \frac{1}{2} \left(q_k - \frac{\lambda_k}{j} \right)$, where $j \in \{\alpha, \beta, \gamma\}$. During period $[0, T)$, species k 's stock decreased from k_0 to 0. In interval $[T, +\infty)$, $k = 0$, $\dot{k} = 0$ and $h_k^* = 0$. Continuity of λ implied that $\liminf_{t \rightarrow T} \lambda_x(t) = \lambda_x(T)$. The necessary conditions for optimal harvest must hold at each time t so $\lambda_k(T) = jq_k$. In interval $[T, +\infty)$, $\lambda_k = 0$ so an expression for $\mu_k(T)$ could be derived.

1. Suppose moose disappeared first. The shadow price of moose did not affect any other species or shadow price when $\dot{x} = 0$, $x = 0$, $h_x = 0$ so the ecosystem followed the dynamics in SYS2M1 with $\mu_y = \mu_z = 0$ as long as no tree species became extinct:

$$\begin{aligned} \dot{y} &= r_y y - y^2 - a_{yz} z - \frac{1}{2} \left(q_y - \frac{\lambda_y}{\beta} \right) \\ \dot{z} &= r_z z + z^2 - a_{zy} y - \frac{1}{2} \left(q_z - \frac{\lambda_z}{\gamma} \right) \end{aligned} \quad (22)$$

$$\begin{aligned}\dot{\lambda}_y &= \rho\lambda_y - \lambda_y(r_y - 2y) + \lambda_z a_{zy} \\ \dot{\lambda}_z &= \rho\lambda_z + \lambda_y a_{yz} - \lambda_z(2r_z z - 3z^2)\end{aligned}$$

When only two species were left, either this remained so forever or at some time $T' > T$ a second species disappeared. Suppose birch disappeared from system (SYS2M1) at time $T' > T$, then $\lambda_y = \beta q_y$ and $\dot{\lambda}_y = 0$ so we could calculate $\mu_y = \frac{\rho\beta q_y + \lambda_z a_{zy}}{(r_y - 2y)} - \beta q_y$, $y \neq \frac{r_y}{2}$ and the system became

$$\begin{aligned}z &= r_z z + z^2 - a_{zy} y - \frac{1}{2} \left(q_z - \frac{\lambda_z}{\gamma} \right) \\ \dot{\lambda}_z &= \rho\lambda_z + \frac{\rho\beta q_y + \lambda_z a_{zy}}{(r_y - 2y)} a_{yz} - \lambda_z(2r_z z - 3z^2)\end{aligned} \quad (\text{SYS2M2})$$

If instead pine disappeared at time T' , $\lambda_z = \beta q_z$ and $\dot{\lambda}_z = 0$ but μ_z could not be calculated from the $\lambda_z = 0$ equation. To insure that $\lambda_z = 0$ we needed to have $\lambda_y = -\frac{\rho\beta q_z}{a_{yz}}$ implying that $\dot{\lambda}_y = 0$ and $\mu_z = -\frac{\rho\beta q_z (r_y - 2y - \rho)}{a_{yz} a_{zy}} - \beta q_z$ the system became

$$\begin{aligned}\dot{y} &= r_y y - y^2 - \frac{1}{2} \left(q_y - \frac{\rho q_z}{a_{yz}} \right) \\ \dot{\lambda}_y &= 0\end{aligned} \quad (\text{SYS2M3})$$

2. Suppose instead birch disappeared first. Then at time T , $\lambda_y = \beta q_y$ and $\mu_y = \frac{\rho\beta q_y - \lambda_x a_{xy} x + \lambda_z a_{zy}}{r_y - a_{yx} x} - \beta q_y$, if $x \neq \frac{r_y}{a_{yx}}$. The system to simulate looked like this:

$$\begin{aligned}x &= x - x^2 + a_{xz} x z - \frac{1}{2} q_x + \frac{\lambda_x}{2\alpha} \\ z &= r_z z^2 - z^3 - a_{zx} x z - \frac{1}{2} q_z + \frac{\lambda_z}{2\gamma} \\ \dot{\lambda}_x &= \rho\lambda_x - \lambda_x(1 - 2x + a_{xz} z) + \lambda_z a_{zx} z \\ \dot{\lambda}_z &= \rho\lambda_z - \lambda_x a_{xz} x + \frac{\rho\beta q_y - \lambda_x a_{xy} x + \lambda_z a_{zy}}{r_y - a_{yx} x} a_{yz} - \lambda_z(2r_z z - 3z^2 - a_{zx} x)\end{aligned} \quad (\text{SYS2B1})$$

Either the forest remained a forest with only pine and moose or at some time

$T' > T$, one of the remaining species disappeared. If moose disappeared at time T' , then $\lambda_x = \alpha q_x$ and $\dot{\lambda}_x = 0$. The shadow price of moose did not affect pine's stock and shadow price so the system became

$$\begin{aligned} \dot{z} &= r_z z^2 - z^3 - \frac{1}{2}q_z + \frac{\lambda_z}{2\gamma} \\ \dot{\lambda}_z &= \rho\lambda_z + \frac{\rho\beta q_y + \lambda_z a_{zy}}{r_y} a_{yz} - \lambda_z (2r_z z - 3z^2) \end{aligned} \quad (\text{SYS2B2})$$

If instead pine disappeared, $\lambda_z = \gamma q_z$ and $\dot{\lambda}_z = 0$. The shadow price of pine did not affect the biomass of moose so the system became

$$\begin{aligned} \dot{x} &= x - x^2 - \frac{1}{2}q_x + \frac{\lambda_x}{2\alpha} \\ \dot{\lambda}_x &= \rho\lambda_x - \lambda_x (1 - 2x) \end{aligned} \quad (\text{SYS2B3})$$

3. If pine disappeared first, the system could be derived in a similar way. At time T , $\lambda_z = \gamma q_z$ and $\mu_z = -\frac{\rho\lambda_z - \lambda_x a_{xz}x + \lambda_y a_{yz}}{a_{zx}x} - \gamma q_z$ provided $x \neq 0$. The system to simulate looked like this:

$$\begin{aligned} \dot{x} &= x - x^2 + a_{xy}xy - \frac{1}{2}q_x + \frac{\lambda_x}{2\alpha} \\ \dot{y} &= r_y y - y^2 - a_{yx}xy - \frac{1}{2}q_y + \frac{\lambda_y}{\beta} \\ \dot{\lambda}_x &= \rho\lambda_x - \lambda_x (1 - 2x + a_{xy}y) + \lambda_y a_{yx}y \\ \dot{\lambda}_y &= \rho\lambda_y - \lambda_x a_{xy}x - \lambda_y (r_y - 2y - a_{yx}x) - \frac{\rho\gamma q_z - \lambda_x a_{xz}x + \lambda_y a_{yz}}{a_{zx}x} a_{zy} \end{aligned} \quad (\text{SYS2P1})$$

Again, either the forest remained a two species forest forever or at some time $T' > T$ one of the remaining species disappeared. Suppose moose disappeared at time T' , then $\lambda_x = \alpha q_x$. Further, $\lim_{x \rightarrow 0} \frac{\rho\lambda_z - \lambda_x a_{xz}x + \lambda_y a_{yz}}{a_{zx}x} = (\rho\lambda_z + \lambda_y a_{yz}) \times (+\infty)$ implying that either λ_y became very negative in which case birch became or λ_y increased very much and birch harvest became equal to zero giving the system.

$$\dot{y} = r_y y - y^2 \quad (\text{SYS2P2})$$

$$\dot{\lambda}_y = - \lim_{x \rightarrow 0} \frac{\rho \lambda_z - \lambda_x a_{xz} x + \lambda_y a_{yz}}{a_{zx} x} a_{zy}$$

Suppose instead birch disappeared at time T' . The shadow price for birch did not affect the stock and the shadow price for moose so the system became:

$$\begin{aligned} \dot{x} &= x - x^2 - \frac{1}{2}q_x + \frac{\lambda_x}{2\alpha} & (\text{SYS2P3}) \\ \dot{\lambda}_x &= \rho \lambda_x - \lambda_x (1 - 2x) \end{aligned}$$

Acknowledgement *Thanks to my supervisor Karl-Göran Mäler for many discussions about the paper. I also thank Kjell Danell, Karl-Gustaf Löfgren, Eric Nævdal, John Pastor, Hans Wallin, Angels Xabadia (this paper's opponent at the Second World Congress of Environmental and Resource Economists, June 2002, Monterey, CA, US), Göran Ågren, and participants in a seminar given at the department of forestry economics at the Swedish University of Agricultural Sciences in Umeå, January 2002. Thanks to the participants of the Meeting of the Theory group of the Resilience Network, May 3-5, 2000 in Belize (especially William Brock and Simon Levin), who gave me valuable comments on an early draft. I gratefully acknowledge funding from the Swedish Council for Forestry and Agricultural Research (SJFR) and the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (Formas).*

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- (l) This paper was presented at the Workshop “Growth, Environmental Policies and Sustainability” organised by the Fondazione Eni Enrico Mattei, Venice, June 1, 2001
- (li) This paper was presented at the Fourth Toulouse Conference on Environment and Resource Economics on “Property Rights, Institutions and Management of Environmental and Natural Resources”, organised by Fondazione Eni Enrico Mattei, IDEI and INRA and sponsored by MATE, Toulouse, May 3-4, 2001
- (lii) This paper was presented at the International Conference on “Economic Valuation of Environmental Goods”, organised by Fondazione Eni Enrico Mattei in cooperation with CORILA, Venice, May 11, 2001
- (liii) This paper was circulated at the International Conference on “Climate Policy – Do We Need a New Approach?”, jointly organised by Fondazione Eni Enrico Mattei, Stanford University and Venice International University, Isola di San Servolo, Venice, September 6-8, 2001
- (liv) This paper was presented at the Seventh Meeting of the Coalition Theory Network organised by the Fondazione Eni Enrico Mattei and the CORE, Université Catholique de Louvain, Venice, Italy, January 11-12, 2002
- (lv) This paper was presented at the First Workshop of the Concerted Action on Tradable Emission Permits (CATEP) organised by the Fondazione Eni Enrico Mattei, Venice, Italy, December 3-4, 2001
- (lvi) This paper was presented at the ESF EURESCO Conference on Environmental Policy in a Global Economy “The International Dimension of Environmental Policy”, organised with the collaboration of the Fondazione Eni Enrico Mattei, Acquafredda di Maratea, October 6-11, 2001
- (lvii) This paper was presented at the First Workshop of “CFEWE – Carbon Flows between Eastern and Western Europe”, organised by the Fondazione Eni Enrico Mattei and Zentrum für Europäische Integrationsforschung (ZEI), Milan, July 5-6, 2001
- (lviii) This paper was presented at the Workshop on “Game Practice and the Environment”, jointly organised by Università del Piemonte Orientale and Fondazione Eni Enrico Mattei, Alessandria, April 12-13, 2002
- (lix) This paper was presented at the ENGIME Workshop on “Mapping Diversity”, Leuven, May 16-17, 2002
- (lx) This paper was presented at the EuroConference on “Auctions and Market Design: Theory, Evidence and Applications”, organised by the Fondazione Eni Enrico Mattei, Milan, September 26-28, 2002
- (lxi) This paper was presented at the Eighth Meeting of the Coalition Theory Network organised by the GREQAM, Aix-en-Provence, France, January 24-25, 2003
- (lxii) This paper was presented at the ENGIME Workshop on “Communication across Cultures in Multicultural Cities”, The Hague, November 7-8, 2002
- (lxiii) This paper was presented at the ENGIME Workshop on “Social dynamics and conflicts in multicultural cities”, Milan, March 20-21, 2003
- (lxiv) This paper was presented at the International Conference on "Theoretical Topics in Ecological Economics", organised by the Abdus Salam International Centre for Theoretical Physics - ICTP, the Beijer International Institute of Ecological Economics, and Fondazione Eni Enrico Mattei – FEEM Trieste, February 10-21, 2003

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