Agriculture, pesticides and the ecosystem

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1. Introduction

Economists have a good understanding of intra-economy interdependence and a mature and powerful methodology of modeling it. When it became evident that economic activities had detrimental impacts on ecological systems (*ecosystems*, for short), environmental economics developed as a branch of externality theory which, however, focused on environment-economy interactions in a rudimentary way only. On the other hand, natural scientists developed models for understanding species interactions in ecosystems, and they also study the impact of economic activities on ecosystems. However, anthropogenic distortions enter their analysis often as exogenous parameter shocks only. It appears, therefore, that in their studies of environment-economy interactions both disciplines, ecology and economics, are biased in opposite directions: Ecologists tend to disregard the complexity of the economic system and economists tend to neglect intra-ecosystem interdependence and ecological repercussions caused by economic activities.

In our view, environment-economy interdependence cannot be satisfactorily studied unless both intra-economy and intra-ecosystem interdependence is explicitly modeled and, in addition, the repercussions set off by one system in the other are captured – including the feedback of these repercussions into the system where the disturbance originated. Natural scientists use to model intra-ecosystem interdependence in dynamic multi-species population models. They apply macro approaches taking populations as basic endogenous variables and hence disregard the interactions of species at the micro level. In contrast, economic modeling is, in general, microfounded relying on maximizing behavior of firms and consumers.

The present paper aims at applying economic methodology to modeling the ecosystem,² following, to some extent, Hannon (1976), Crocker and Tschirhart (1992) and Tschirhart

 2 For a survey and critical assessment of economic approaches to ecosystem analysis see Eichner and Pethig (2001).

¹ This type of modeling is surveyed by Murray (1993) and Brown and Rothery (1993).

(2000). It offers, on that basis, a formal analysis of environment-economy interdependence. The ecosystem submodel of the short period is based on the idea that the representative organism of each species behaves 'as if' it maximizes its net (or stored) energy. Our approach differs from that of Hannon, Crocker and Tschirhart in how the organisms' "production function" (physiological function) are specified and in the concept of short-run ecological equilibrium. We don't use equilibrating prices as the authors mentioned above but assume, instead, that given the activities of all other organisms each organism acts as if it optimizes its costly offensive and defensive activities (Nash-behavior).

We develop a three-species model of an ecosystem linked to a simple model of the economy with agricultural production and consumption. The three species form a unidirectional non-circular food chain: buzzards feed on mice, mice feed on grain, and grain 'feeds' on solar energy.³ There is a fourth species, in fact, the humans, who feed on grain, too. Humans are given the option to intervene into the ecosystem in three different ways. They can increase the growth (and harvest) of grain by farm labor input; they can use pesticides to diminish the mice population so that mice leave more grain for harvesting; and they can use resources, referred to as labor for simplicity, to improve, or prevent deterioration of, the buzzard habitat - with the consequence that the buzzard population prospers and buzzards prey more mice. Particular attention will be placed on the derivation of a short-run ecological equilibrium which will be shown to depend on the set of human activities. Thus we establish environment-economy interdependence and require both systems to settle for an equilibrium simultaneously. From the economist's perspective the ecosystem creates positive and negative externalities (Crocker and Tschirhart, 1992) which are particularly pronounced when consumers have 'green' preferences. But note also that in our model economic activities can be viewed to create externalities in the ecosystem.

Section 2 of the paper elaborates on the ecological interdependence as well as on the concept and the properties of short-run ecological equilibrium. Section 3 combines the ecosystem model with a model of the economy and characterizes the Pareto efficient allocation and section 4 discusses both the inefficiencies of the competitive economy and the possibility to restore efficiency through corrective taxes or subsidies. The tax incidence analysis of section 5 shows the impact of tax changes on both the economy and the ecosystem yielding additional

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³ This interpretation of the food chain is more allegoric than realistic in nature. Our main objective is to elaborate on a new method of studying ecosystem-economy interdependence.

information on the type of distortions caused by the externalities. Section 6 introduces stock-flow relationships and sketches how short-run ecological equilibria are linked to ecosystem dynamics which may or may not drive the ecosystem toward a steady state (long-run ecological equilibrium). Section 7 concludes.

2. Ecological interdependence and short-run ecological equilibrium

We now envisage an ecosystem in a short period (and stick to the short term until section 6) in which the populations of all species are given. The focus is on representative organisms of all species and the *net incremental energy* they are able to develop during the period under consideration. These net energies are denoted g for grain, m for mice and b for buzzards. For brevity, we refer to the representative organism of a species as *organism* v, for v = g, m, b. The organisms' net energies are, respectively,

$$g = \left(\widetilde{e}_{og} x_{og}^d - \widetilde{e}_{g} x_{gm}^s - \widetilde{r}_{ga}\right) \left(1 - \alpha_g\right),\tag{1a}$$

$$m = T(m_p, p)(\widetilde{e}_{gm}x_{gm}^d - \widetilde{e}_m x_{mb}^s - \widetilde{r}_{mf} - \widetilde{r}_{ma})(1 - \alpha_m), \tag{1b}$$

$$b = \left(\widetilde{e}_{mb} x_{mb}^d - \widetilde{r}_{bf}\right) (1 - \alpha_b), \tag{1c}$$

where \tilde{e}_j = energy per unit biomass of organism i (i = g, m); $e_j > 0$ and constant

 \tilde{e}_{ij} = energy intake of predator j per unit of biomass from prey I; $e_{ij} > 0$ and constant

 α_i = energy used up for respiration and maintenance per unit of (gross) energy, $\alpha_i \in]0,1[$

 x_{ij}^d = biomass of prey *i* demanded by predator *j*

 x_{ij}^{s} = biomass of prey *i* supplied to predator *j*

 \tilde{r}_{ij} = offensive or preying effort of predator *i* in terms of own energy spent

 \widetilde{r}_{ia} = averting or defensive effort of prey *i* in terms of own energy spent

p = amount of pesticides applied to grain (fields)

$$m_p = \left(\widetilde{e}_{gm} x_{gm}^d - \widetilde{e}_m x_{mb}^s - \widetilde{r}_{mf} - \widetilde{r}_{ma}\right) (1 - \alpha_m)$$

= net energy of organism m when no pesticides are applied

$$T(m_p, p) := [1 - \delta(m_p)\theta(p)]$$
 with $\delta(m_p)$ $\begin{cases} = 1, & \text{if } m_p \ge 0, \\ = -1 & \text{otherwise.} \end{cases}$

In $T(m_p, p)$, $\theta(p)$ is the fraction of energy of the representative mouse deleted by pesticides p dotted about the grain fields. The function θ satisfies $\theta(p) \ge 0$ with $\theta(p) = 0$ for p = 0 and $\theta_p > 0$, $\theta_{pp} \ge 0$. Note that $T(m_p, p) < 0$ if and only if $m_p > 0$ and $\theta(p) > 1$.

Denote by n_v for v = g, m, b the (constant) population of species v, i.e. the number of its organisms in the short period under consideration. Since biomass intake by a predator must equal the biomass outflow from its prey we clearly require

$$n_{g}x_{gm}^{s} = n_{m}x_{gm}^{d} \text{ and } n_{m}x_{mb}^{s} = n_{b}x_{mb}^{d}$$
 (2)

It is assumed that all predators' demands prevail. Therefore x_{gm}^s and x_{mb}^s are substituted in (1) by $(n_m/n_g)x_{gm}^d$ and $(n_b/n_m)x_{mb}^d$, respectively, keeping in mind that the latter are the decision variables of species m and b, respectively. In addition, we suppress all (constant) populations and simplify the notation by setting $e_{ij} := \widetilde{e}_{ij} \left(1 - \beta_i \right)$, $e_j := \widetilde{e}_j \left(1 - \beta_j \right)$, $r_{ia} := \widetilde{r}_{ia} \left(1 - \beta_i \right)$ and $r_{if} := \widetilde{r}_{if} \left(1 - \beta_i \right)$. Thus (1) is transformed into

$$g = e_{og} x_{og}^{d} - e_{g} x_{gm}^{d} - r_{ga}, (3a)$$

$$m = T(m_p, p)(e_{gm}x_{gm}^d - e_mx_{mb}^d - r_{mf} - r_{ma}),$$
(3b)

$$b = e_{mb}x_{mb}^d - r_{bf}. ag{3c}$$

The next step is to introduce averting behavior by⁴

$$a_g = A^g(n_g, n_m, r_{ga}), \quad a_m = A^m(n_m, n_b, r_{ma}),$$
 (4)

$$x_{o\sigma}^d = y_{o\sigma}, \quad x_{om}^d = a_{\sigma} y_{om} \quad \text{and} \quad x_{mb}^d = a_m y_{mb},$$
 (5)

where $A^{\nu}(\cdot) \in]0, I]$ with $A^{\nu}(0) = I$, and $A^{\nu}_{rr} > 0$. The role of populations in (4) is straightforward. The success of a given averting effort (r) is the greater, ceteris paribus, the larger the own population is (because it is then the more likely that the predator catches another organ-

⁴ A minus or plus underneath an argument of a function indicates the sign of the pertinent partial derivative.

ism) and the smaller the predator population is (because a predator-prey encounter is then less likely). In the sequel we leave the impact of populations aside since they are constant in the short period. Regarding the averting effort, the idea behind (4) and (5) is to consider the biomass of a prey organism a predator takes in as being determined by both the predator's offensive activity (y) and the prey's averting activity (a). In other words, a_g and a_m reflect the impact of defensive efforts of preys on the predators' preying success, x. y_{og} , y_{gm} and y_{mb} are the variables under control of the respective predators. For example, if m does not undertake any averting effort $(r_{ma} = 0)$, then $a_m = 1$ and $x_{mb}^d = y_{mb}$. Hence y_{mb} is the buzzard's intake of mice in the absence of defensive activities by mice If, however, $r_{ma} > 0$, then $a_m < 1$ and the buzzards' intake of mice is $x_{mb}^d < y_{mb}$. It remains to specify the determinants of the 'defenseless intakes' of predators:

$$y_{og} = Y^{og}(\ell_g, n_m, m, s)$$
+ - - +

$$y_{gm} = Y^{gm}(g, n_g, n_m, r_{mf})$$
(6b)

$$y_{mb} = Y^{mb}(\ell_b, m, n_m, n_b, r_{bf})$$
(6c)

 Y^{og} is the farmers' grain growing 'technology'. He combines seeds, s, and farm labor, ℓ_g , to expose the grain to sunlight and to other nutrients like water, minerals etc. available in the ecosystem (but not entering our model). $Y_m^{og} < 0$ and $Y_{n_m}^{og} < 0$ means that mice impair the cultivation of grain not only through feeding on grain but also in other ways. Mice is perhaps not a convincing example of an animal species doing harm to plants independent of and in addition to feeding but we find it worthwhile to explore the implications of such a hypothesis (see footnote 1). Anyway, it is easy to 'switch off' this effect by simply substituting $p[\cdot] = 0$ for $Y_m^{og} < 0$.

 $Y^{gm}(\cdot)$ is the grain 'harvested' by the representative mouse if grain refrains from averting behavior altogether. The amount of mouse biomass preyed depends on the buzzard's hunt-

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⁵ Mice is perhaps not a convincing example of an animal species doing harm to plants independent of and in addition to feeding but we find it worthwhile to explore the implications of such a hypothesis (see footnote 1). Anyway, it is easy to 'switch off' this effect simply by setting $Y_m^{og} = Y_{n_m}^{og} = 0$.

ing effort, on the abundance of net mouse energy and on the farmers' (or other humans') maintenance of the buzzard habitat, ℓ_b . The impact of populations on the technologies (6b) and (6c) is similarly interpreted as in (4). Prey abundance eases the predator's business of preying (with given predation effort) while an increase in the predator's own population reduces the preying success, ceteris paribus, because the individual predator faces competition from its own kind.

Recall, however, that these hypotheses are ineffective in the present context since we deal with the short period in which populations are constant. To avoid clutter we therefore suppress all populations in (4) and (6) in the following analysis, but we will return to this issue in section 6.

Inserting (4), (5) and (6) in (7) yields

$$G^{o}(\ell_{g}, r_{ga}, y_{gm}) := e_{og}Y^{og}(\ell_{g}, m, s) - e_{g}A^{g}(r_{ga})y_{gm} - r_{ga}$$
(7a)

$$M^{o}(a_{g}, g; p, r_{ma}, r_{mf}, y_{mb}) := T(m_{p}, p) [e_{gm}a_{g}Y^{gm}(g, r_{mf}) - e_{m}A^{m}(r_{ma})y_{mb} - r_{mf} - r_{ma}]$$
 (7b)

$$B^{o}\left(a_{m}, \ell_{b}, m, r_{bf}\right) = e_{mb}a_{m}Y^{mb}\left(\ell_{b}, m, r_{bf}\right) - r_{bf}$$

$$(7c)$$

There are four different types of arguments in the functions G^o , M^o and B^o . First, the organisms' own offensive and/or defensive efforts (r); second, other organisms' predation (y) or defense (a) variables; third, other organisms' net energies; and finally, human activities ℓ_b , ℓ_g p and s. Obviously, the economic activities form links from the economy to the ecosystem. They will be kept constant in the present section but endogenized later and then complemented by links from the ecosystem to the economy.

Recall from (6) that the net energy of its prey impacts on the predator's productivity of hunting $(g \text{ in } M^o \text{ and } m \text{ in } B^o)$. We assume that predators take these variables as given because it is plausible that they ignore the indirect effect they exert themselves on the net energy of their prey via their own predation. We also assume that each prey takes as given the demand for its own biomass and that each predator takes as given the impact on its predation success of its prey's averting activity. As a consequence, the only variables each organism controls are its own offensive and/or defensive efforts which it chooses as if it maximizes its own net energy – given all other organisms' offensive and/or defensive activities.

Our suggestion that organisms behave 'as if' they maximize their net energy is in line with Hannon (1976), Crocker and Tschirhart (1992), Tschirhart (2000) and others. But while these authors model organisms as price takers the present model assumes Nash behavior in the absence of prices. To be more specific, we conceive of a non-cooperative game between the representative organisms of grain, mice and buzzards. The players' strategies are:

organisms	grain	mice	buzzards	
strategies	a_g	a_m, y_{gm}	\mathcal{Y}_{mb}	

To determine their own best response to the other players' given strategies the organisms solve, respectively,

$$\max_{r_{ga}} G^{o}(\ell_{g}, r_{ga}, y_{gm}), \tag{8a}$$

$$\max_{r_{ma}, r_{mf}} M^{o}(a_{g}, g; p, r_{ma}, r_{mf}, y_{mb}),$$
(8b)

$$\max_{r_{bf}} B^{o}(a_{m}, \ell_{b}, m, r_{bf}). \tag{8c}$$

Assuming that the functions G^o , M^o and B^o are strictly concave in r_{ga} , $\left(r_{ma}, r_{mg}\right)$ and r_{bf} , respectively, the maximizers can be determined as functions

$$r_{ga} = R^{ga}(y_{gm}), \quad r_{ma} = R^{ma}(y_{mb}), \quad r_{mf} = R^{mf}(a_g), \quad r_{bf} = R^{bf}(a_m).$$
 (9)

The next step is to combine (9) with (4) and (7) to obtain the best responses

$$a_g = A^g \left[R^{ga} \left(y_{gm} \right) \right], \quad y_{gm} = Y^{gm} \left[g, R^{mf} \left(a_g \right) \right], \tag{10a}$$

$$a_m = A^m [R^{ma}(y_{mb})], \quad y_{mb} = Y^{mb} [m, R^{bf}(a_m), \ell_b],$$
 (10b)

Since our model describes a unilateral non-circular food chain, it is not surprising that the game disintegrates in two subgames specified in (10a) and (10b). A Nash equilibrium of these subgames is attained when both players' strategies are best responses to the strategy of their opponents. The equilibrium strategies (a_g^*, y_{gm}^*) and (a_m^*, y_{mb}^*) are hence determined by solving the two equations in (10a) and (10b), respectively. Total differentiation reveals that there are functions \overline{A}^g , \overline{A}^m , \overline{Y}^{gm} and \overline{Y}^{mb} such that

$$a_g^* = \overline{A}^g(g), \quad y_{gm}^* = \overline{Y}^{gm}(g), \quad a_m^* = \overline{A}^m(\ell_b, m), \quad y_{mb}^* = \overline{Y}^{mb}(\ell_b, m).$$
 (11)

The signs of the derivatives given in (11) are unambiguous except for $\overline{Y}_g^{gm} > 0$ and $\overline{Y}_m^{mb} > 0$. To see this, consider y_{gm} from (10a) and a_g^* from (11): $y_{gm} = \overline{Y}^{gm}(g) = Y^{gm}\{g, R^{mf}[\overline{A}^g(g)]\}$. Total differentiation yields, after some rearrangement of terms,

$$Y_g^{gm} = Y_g^{gm} + Y_r^{gm} \cdot R_a^{mf} \cdot \overline{A}_g^g . \tag{12}$$

For interpreting (12) suppose the net energy of grain rises. Then grain steps up its defensive effort $(\overline{A}_g^g < 0)$ which has a negative but indirect effect on mice predation productivity. On the other hand, by assumption (6a) increasing grain energy has a direct positive effect on mice predation $(Y_g^{gm} > 0)$. It appears to be a plausible assumption that the positive direct effect overcompensates the negative indirect effect.

The last step is to determine the equilibrium net energies by combining (7) with (9) and (11). We obtain

$$g = G^{o}\left\{R^{ga}\left[\overline{Y}^{gm}(g)\right], \overline{Y}^{gm}(g), \ell_{g}\right\}$$
(13a)

$$m = M^{o} \left\{ R^{ma} \left[\overline{Y}^{mb}(\ell_{b}, m) \right], R^{mf} \left[\overline{A}^{g}(g) \right], \overline{Y}^{mb}(\ell_{b}, m), g, p \right\}$$
(13b)

$$b = B^{o}\left\{R^{bf}\left[\overline{A}^{m}(\ell_{b}, m)\right], \ \overline{A}^{m}(\ell_{b}, m), m, \ell_{b}\right\}$$
(13c)

As shown in the appendix solving (13) for all organisms' net energies yields

$$g = \hat{G}(\ell_g, m, s), \tag{14a}$$

$$m = \hat{M}(g, \ell_g, p), \tag{14b}$$

$$b = \hat{B}(\ell_b, m). \tag{14c}$$

The signs of the partials in (14) are clear cut except for \hat{M}_g , \hat{B}_ℓ and \hat{B}_m . The signs we assigned to \hat{M}_g , \hat{B}_ℓ , and \hat{B}_m in (14) result if the offensive activities react to the variables g, ℓ_b and m,

⁶ The capacity of plants to discourage their predators from feeding on them is small if not even zero. We introduced the assumption $A_r^g < 0$ primarily to demonstrate the generic structure of the food chain model. \overline{Y}_m^{mb} is given by an expression analogous to (12). In this case averting behavior of mice is significant but we find it still realistic that the indirect is of second order only.

respectively, stronger than the defensive variables. $\hat{M}_g > 0$ presupposes, in addition, $\theta(p) \le I$ in case of $m_p > 0$. More details are presented in the appendix.

Solving the equations (14) for g, m and h finally yields the short-run ecological equilibrium. The solution (b_0, g_0, m_0) to (14) is illustrated in figure 1 for given $\ell_b = \ell_{b0}$, $\ell_g = \ell_{g0}$ and $p = p_0$.

Figure 1: Short-run ecological equilibrium

Figure 1 also shows the impact on the ecological system of increasing the use of pesticides from p_0 to $p_1 > p_0$. The point of intersection of the curves $\hat{G}(\cdot)$ and $\hat{M}(\cdot)$ shifts from Q_0 to Q_1 implying that using more pesticides does not only hurt mice but also buzzards: The net energy of organism m shrinks from m_0 to m_1 and that of organism m shrinks from m_0 to m_1 and that of organism m shrinks from m_0 to m_1 and that of organism m shrinks from m_0 to m_1 leaves the mice population with reduced but still positive growth whereas the buzzards population shrinks m_1 Note also that the additional use of pesticides increases grain net energy.

Another interesting information can be attained through comparative static analysis as follows: We start again with an initial equilibrium for given $(\ell_{g0}, \ell_{b0}, p_0)$. But now we leave ℓ_{g0} and p_0 unchanged and raise, instead, the labor input from ℓ_{b0} to $\ell_{b1} > \ell_{b0}$. In figure 1, ℓ_{b1} has been chosen such that the new \hat{M} -curve intersects the \hat{G} -curve in Q_1 (as before, when p rather than ℓ_b was increased, c. p.). Hence the impact on grain is the same as in case of increasing p, but the buzzard net energy is still positive (it even increased from b_0 to b_2 !). Our model thus demonstrates that farmers have at their disposal two different strategies for enhancing farming productivity: fighting against nature (pesticides) or collaborating with nature (buzzard habitat maintenance). Presupposing that farmers have a good knowledge of both options (which cannot be taken far granted) their choice will depend on comparative costs. This issue will be re-addressed later in this paper.

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⁷ This effect can be traced back to the assumption $Y_m^{og} < 0$ in (6a). If $Y_m^{og} = 0$ one has $\hat{G}_m = 0$ so that the \hat{G} -curve is vertical in figure 1.

It remains to investigate the algebraic solution of (14). For that purpose we differentiate (14b) and (14c) to obtain

$$dg = \frac{1}{1 - \hat{G}_{m} \hat{M}_{g}} \left[\hat{G}_{\ell} d\ell_{g} + \hat{G}_{m} \hat{M}_{\ell} d\ell_{b} + \hat{G}_{m} \hat{M}_{p} dp \right].$$

$$dm = \frac{1}{1 - \hat{G}_m \hat{M}_g} \left[\hat{M}_g \hat{G}_\ell d\ell_g + \hat{M}_\ell d\ell_b + \hat{M}_p dp \right].$$

From this information we infer that there are functions G and M such that

$$g = G(\ell_b, \ell_g, p, s) := \hat{G}[\ell_g, \hat{M}(g, p, \ell_b), s],$$
(15a)

$$m = M(\ell_b, \ell_g, p, s) := \hat{M} [\hat{G}(\ell_g, m, s), p, \ell_b].$$

$$(15b)$$

Finally, we combine (14a) and (15b) to obtain

$$b = B(\ell_b, \ell_g, p, s) := \hat{B}[\ell_b, M(\ell_b, \ell_g, p, s)].$$
(15c)

where $\partial B/\partial \ell_b =: B_{\ell_b} = \hat{B}_{\ell} + \hat{B}_{m} M_b$. The indeterminacy of the sign of B_{ℓ_b} can be easily illustrated in figure 1. The dashed curve in the left panel is the graph of $\hat{B}(m,\ell_{bl})$. The increase in labor input from ℓ_{b0} to ℓ_{bl} is assumed to have shifted the \hat{B} -curve such that $b_2 > b_0$, hence $B_{\ell_b} > 0$ (i. e. \hat{B}_{ℓ} overcompensates $\hat{B}_m M_b$). If the dashed line representing function $\hat{B}(m,\ell_{bl})$ would have been shifted further up, but still below the solid line depicting the graph of $\hat{B}(m,\ell_{b0})$ then we would have had $b_2 < b_0$, hence $B_{\ell_b} < 0$.

It conforms to our intuition that all farming activities, ℓ_b , ℓ_g , p and s boost the growth of grain, but it is less intuitive that in (15b) and (15c) farm work and seed also foster mice and buzzards. In the real world, land needed for farming reduces and/or deteriorates the habitat of mice and buzzards. If that observation were included in our formal model, farm work and seed would probably turn out to be less beneficial to the ecosystem.

In view of (15) our results on short-run ecological equilibrium and its properties are now summarized in

Proposition 1:

- (i) For any given economic activities (ℓ_b, ℓ_g, p, s) there is a unique short-run ecological equilibrium.
- (ii) Suppose one of the economic activities is stepped up, ceteris paribus. Then
 - an increase in farm labor input (ℓ_g) and grain seed (s) benefits all species;
 - an increased support for buzzards (ℓ_b) has a positive effect on grain, a negative effect on mice and an ambiguous effect on buzzards;
 - an increased use of pesticides (p) benefits grain but hurts mice and buzzards.
- (iii) If the use of pesticides (p) is successively stepped up, the growth of grain is enhanced but mice and buzzards are eventually driven out of the ecosystem.
- (iv) If the support of buzzards (ℓ_b) is successively increased, grain benefits and mice vanish eventually; the population of buzzards may grow temporarily but will eventually be forced to leave the region when there are no more mice.

3. Efficient farming in the integrated ecosystem-economy model

In the previous section we investigated the short-run ecological equilibrium, but we also provided the interface of ecosystem-economy interdependence via the economic activities (ℓ_b, ℓ_g, p, s) . We also demonstrated how (parametric) changes of these economic activities impacted on the ecosystem. Now we turn to ecological-economic interaction by developing a simple model of the *economy* with several links to the ecosystem.

The purpose of grain farming is to harvest the entire grain biomass for (human) consumption. Hence function G in (15a) represents the *production function for grain*. To reduce complexity we assume that a constant amount of harvested grain is set aside as seed for growing grain in the next period. Pesticides are assumed be produced with labor input ℓ_p according to the linear function

⁸ For simplicity we dispense with modeling grain as an intermediate good to be transformed into final consumer goods say 'bread'

⁹ In a more encompassing approach the amount of seed to be retained would be included in the social planer's or the farmers' intertemporal optimization calculus

$$\ell_p = c_p p \quad (c_p > 0 \text{ and constant}).$$
 (16)

There are n_c consumers facing the time constraint

$$I = z_i + \ell_i \qquad \qquad i = 1, \dots, n_c, \tag{17}$$

where ℓ_i is consumer i's labor supply and z_i is his or her demand for leasure.

The consumer's strictly quasi-concave utility is

$$u_{i} = U^{i} \left(b, g_{i}, m, z_{i} \right) . \tag{18}$$

The individual consumer considers the net energies of mice and buzzards as given. But he or she need not be indifferent with respect to the state of the ecosystem (as represented by g and m). It is conceivable that for v=m, b the marginal utility U_v^i is zero, positive or negative. We will restrict our attention to *green preferences*, i. e. $U_v^i > 0$ for v=b, m and compare this scenario with an economy where consumers don't care about the ecosystem: $U_v^i = 0$ for v=b, m.

The model of the economy is completed by introducing the aggregate constraint for labor,

$$\sum_{i=1}^{n_c} \ell_i \ge \ell_b + \ell_g + \ell_p . \tag{19}$$

Figure 2: The integrated ecosystem-economy model

Figure 2 illustrates the structure of the integrated ecosystem-economy model depicting the ecosystem and the economy in its right and left part, respectively, and showing the interface of both systems in the middle.

To simplify the exposition we assume that all consumers are identical. This allows us to invoke (14), (16), (17) and (19) to rewrite (18):

$$u = U \left[\frac{G(\ell_b, \ell_g, p)}{n_c}, M(\ell_b, \ell_g, p), B(\ell_b, \ell_g, p), I - \frac{\ell_b - \ell_g - c_p p}{n_c} \right]$$
(18')

To characterize an efficient allocation we maximize (18') with respect to ℓ_b , ℓ_g and p. For the maximization problem to be well-behaved we need to assume that the functions G, M and B

are concave. Our focus is on solutions satisfying $\ell_g > 0$ and $\ell_b \ge 0$, $p \ge 0$. The pertinent first order conditions are

$$\frac{dU}{d\ell_b} = \left[U_g G_{\ell_b} \frac{1}{n_c} + U_m M_{\ell_b} + U_b B_{\ell_b} - U_z \frac{1}{n_c} \right] \le 0 \quad \text{and} \quad \ell_b[\cdot] = 0,$$
 (20a)

$$\frac{dU}{d\ell_{g}} = U_{g}G_{\ell_{g}}\frac{1}{n_{c}} + U_{m}M_{\ell_{g}} + U_{b}B_{\ell_{g}} - U_{z}\frac{1}{n_{c}} = 0,$$
(20b)

$$\frac{dU}{dp} = \left[U_g G_p \frac{1}{n_c} + U_m M_p + U_b \cdot B_p - c_p U_z \frac{1}{n_c} \right] \le 0 \text{ and } p[\cdot] = 0.$$
 (20b)

Divide (20) by $U_g > 0$, define the marginal willingness to pay for V in terms of grain by $W_{vg} := \frac{U_v}{U_g}$ for v = b, m, z and rewrite (20) as

$$\left[G_{\ell_b} + n_c W_{mg} M_{\ell_b} + n_c W_{bg} B_{\ell_b}\right] \le W_{zg} \quad \text{and} \quad \ell_b[\cdot] = 0,$$
(21a)

$$G_{\ell_g} + n_c W_{mg} M_{\ell_g} + n_c W_{bg} B_{\ell_g} = W_{zg},$$
(21b)

$$\left[G_p + n_c W_{mg} M_p + n_c W_{bg} B_p\right] \le c_p W_{zg} \quad \text{and} \quad p[\cdot] = 0.$$
(21c)

In (21) the terms $n_c W_{mg} M_v$ and $n_c W_{bg} B_v$ for $v = \ell_b$, ℓ_g , p are aggregate marginal values consumers attach to the economic activity v for its impact on mice and buzzards, respectively. Formally these terms are summation conditions as in Samuelson's well-known rule for the efficient allocation of a pure public good. An adequate interpretation in the present context is that for an allocation of the economic activities ℓ_b , ℓ_g and p to be efficient it is necessary to also account for the indirect marginal benefits and costs, economic activities generate via their impact on the ecosystem. In view of this interpretation, the left sides of (21) represent total direct and indirect (net) benefits of activity v and the right side shows marginal labor costs (all terms of grain). The information (21) is summarized in

Proposition 2:

(i) Suppose, consumers are indifferent with respect to the ecosystem $\left(W_{mg} = W_{bg} = 0\right)$. Then it is efficient to use every input in growing grain such that its marginal productivity

equals its marginal cost (in terms of grain) If the marginal productivity falls short of marginal cost, it is efficient not to use the input at all.

- (ii) Suppose, consumers' preferences are green $(W_{mg}, W_{bg} > 0)$.
 - (α) It is not efficient to use pesticides unless their marginal productivity (at p=0) is sufficiently larger than marginal cost to compensate for its negative side effects on mice and buzzards.
 - (β) Efficient buzzard habitat maintenance may be at about the same scale as in case consumers don't care about the ecosystem because its positive effect on buzzards is accompanied by a negative side effect on mice. If $W_{bg} > 0$ and $W_{mg} \leq 0$, may be efficient to foster buzzards even if the marginal productivity (at $\ell_b = 0$) falls short of marginal labor cost.

Even though (21) does not allow for an immediate comparison of allocative efficiency in economies with and without green preferences, the thrust of (21) is that the greening of preferences leads to increased farming $(\ell_g \uparrow)$, reduced use of pesticides $(p \downarrow)$ and an ambiguous change in buzzards habitat care $(\ell_b \uparrow \downarrow)$.

4. Competitive markets and taxes

Suppose now there are competitive markets for pesticides, grain and labor with market prices q_p , q_g and q_ℓ respectively. Grain is chosen as numeraire $(q_g \equiv l)$. There is also a tax t_p on the sales of pesticides and a payroll tax/subsidy t_v on labor input for v = b, g. With technology (15) zero profit is a necessary equilibrium condition in the production of pesticides:

$$q_p = q_\ell c_p. (22)$$

The farmers' grain production function is (15a). As in the last section we keep grain seed constant and therefore it. With this simplification farmers solve the problem

$$\begin{array}{ll}
\text{Maximize } G(\ell_b, \ell_g, p) - (q_\ell + t_g)\ell_g - (q_\ell + t_b)\ell_b - (q_p + t_p)p. \\
(\ell_b, \ell_g, p)
\end{array} \tag{23}$$

The pertinent first order conditions are

$$G_{\ell_b} - t_b \le q_{\ell}$$
 and $\ell_b \cdot (G_{\ell_b} - t_b - q_{\ell}) = 0$, (24a)

$$G_{\ell_g} - t_g = q_{\ell}$$
 (assuming $\ell_g > 0$), (24b)

$$G_p - t_p \le c_p q_\ell$$
, and $p \cdot (G_p - t_p - c_p q_\ell) = 0$. (24c)

The representative consumer solves the Lagrange problem

$$L = U\left(\frac{g}{n_c} m, b, 1 - \ell\right) + \lambda \left(q_{\ell} \ell + \tau - \frac{g}{n_c}\right)$$
(25)

taking m and b as given. τ denotes total tax revenue that is recycled to the consumers in a lump sum fashion. In case of an interior solution the consumer's optimality condition is

$$W_{zg} = q_{\ell}$$
 (optimum consumption) (26)

Now we combine (26) and (24) to compare the result with (19).

Proposition 3: The competitive market allocation is efficient, if and only if it is supported by tax/subsidy rates

$$t_b^* = n_c W_{mg} M_{\ell_b} + n_c W_{bg} B_{\ell_b} , t_g^* = n_c W_{mg} M_{\ell_g} + n_c W_{bg} B_{\ell_g} , t_p^* = n_c W_{mg} M_p + n_c W_{bg} B_p . (27)$$

In case of green preferences t_g^* is a subsidy, t_p^* is a tax and t_b^* may be either a subsidy or a tax or zero.

While the necessity of taxing pesticides was to be expected, it is rather surprising that efficiency requires to subsidize farm work. As observed in our comment on (15), the model appears to overestimate the ecological value of farm work because it ignores the ecological opportunity costs of grain growing. Another intriguing property of the efficient allocation is that different uses of labor are subject to differential tax treatment. Quite obviously, such a tax/sub-sidy proposal would hardly have a great appeal in the political arena. Observe finally that if $W_{mg} = W_{bg} = 0$ then the market allocation is efficient in the absence of any taxes or subsidies.

However, this conclusion was arrived at under the assumption that farmers have a complete understanding of the grain production function from (15a) including the impact on grain production of buzzards habitat maintenance and that, moreover, farmers themselves carry out the necessary habitat maintenance (*green* farming). They may fail to do so either because they

ignore the productivity effect of fostering buzzards (conventional farming) or limited property rights prevent them from caring for the buzzards because the grain fields they own are only a small segment of the buzzards' habitat. In both cases (23) is solved under the additional constraint $\ell_b \equiv 0$. Clearly, provided that $\ell_b = 0$ is efficient, conventional farming can be made efficient by implementing the tax rates t_g^* and t_p^* from proposition 3, and simply ignore t_b^* . If, however, $\ell_b > 0$ is necessary for Pareto efficiency, conventional farming will cause allocative distortions, and there does not exist a tax-subsidy scheme to restore efficiency. The reason is that the solution to (23) subject to $\ell_b \equiv 0$ implies $G_b|_{\ell_b=0} > q_\ell = W_{zg}$. This distortion cannot be removed by setting $t_g = t_g^*$ and $t_p = t_p^*$. 10

If farmers do understand the impact of buzzards on grain cultivation but are not able to care for the buzzards habitat themselves, some kind of cooperative arrangement between farmers and the owners of the habitat would be necessary to provide for efficient habitat maintenance. In case the habitat is made up of public lands and forests, governments are called for to provide an appropriate 'ecosystem-infrastructure' for grain farming.

If tax rates don't attain their Pareto efficient levels the comparison of marginal conditions prevailing in the Pareto optimum on the one hand and in competitive equilibrium on the other hand doesn't allow for straightforward conclusions about how the equilibrium allocation deviates from the optimum. To elicit additional information we will therefore investigate how the market allocation responds to successive tax rate changes. To keep the comparative statics simple, we restrict our attention to the case where B_{ℓ_b} is Pareto efficient, so that we can ignore ℓ_b as an argument in G altogether. For further analytical relief it is assumed that G is linear homogeneous in ℓ_g and p.

5. Tax incidence

If $\ell_g > 0$ and p > 0 in profit-maximizing production of grain, then (24b) and (24c) imply

$$\frac{G_p}{G_g} = \frac{c_p q_\ell + t_p}{q_\ell + t_g}, \qquad \text{(marginal productivity pricing)}$$
 (28)

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¹⁰ There is a second-best tax-subsidy scheme (t_g^o, t_p^o) , but our conjecture is that the pertaining quantity of pesticides, p_o , is greater than the Pareto efficient quantity p^* .

and

$$g = (q_t + t_g)\ell_g + (c_p q_\ell + t_p)p, \qquad \text{(zero profit condition}^{11})$$
 (29)

The representative consumer solves (25) with $\ell_b \equiv 0$ and hence obeys (26). The equations (26), (28) and (29) along with

$$\ell_g + c_p p + n_c z = n_c$$
 (labor market equilibrium) (30)

$$g = G(\ell_g, p)$$
 (production function) (31)

determine the equilibrium values q_ℓ , g, p, ℓ_g and z for any given pair of tax rates (t_g, t_p) . To investigate the impact of small changes in these tax rates the equations (25) - (29) have to be totally differentiated. For further analytical convenience we assume that the utility function U is homothetic in g and z and weakly separable in the pairs of arguments (g, z) and (m, b). With this specification, the application of the so-called 'hat calculus' $(\hat{v} = dv/v)$ turns (26) - (31) into

$$\hat{g} - \hat{z} = \sigma_D \hat{q}_\ell \,, \tag{26'}$$

$$\hat{p} - \hat{\ell}_g = -\theta_\ell \hat{q}_\ell + \theta_g \hat{t}_g - \theta_p \hat{t}_p , \qquad (28)$$

$$\hat{g} = (I - \mu)\hat{q}_{\ell} + \lambda \hat{\ell}_g + (I - \lambda)\hat{p} + \mu_g \hat{t}_g + \mu_p \hat{t}_p, \qquad (29)$$

$$\hat{z} = -\rho_g \hat{\ell}_g - \rho_p \hat{p}, \tag{30'}$$

$$\hat{g} = \lambda \hat{\ell}_{\sigma} + (I - \lambda)\hat{p} . \tag{31'}$$

where σ_D = elasticity of substitution in demand;

 σ = elasticity of substitution in the production of grain;

$$\theta_g := \frac{\sigma t_g}{\left(q_\ell + t_g\right)} > 0 \quad \text{and} \quad \theta_p := \frac{\sigma t_p}{\left(q_p + t_p\right)} > 0 ;$$

$$\theta_{\ell} := \sigma \left(\frac{q_p}{q_p + t_p} - \frac{q_{\ell}}{q_{\ell} + t_g} \right) = \left(\frac{q_p}{t_p} \theta_p - \frac{q_{\ell}}{t_g} \theta_g \right) = \frac{q_{\ell} \left(c_p t_g - t_p \right)}{\left(q_p + t_p \right) \left(q_{\ell} + t_g \right)} < 0;$$

¹¹ (29) is a necessary equilibrium condition, because G is assumed to be linear homogenous.

$$\mu_g := \frac{t_g \ell_g}{g} < 0, \ \mu_p := \frac{t_p p}{g} > 0, \ \mu = \mu_g + \mu_p \text{ and } I - \mu > 0;$$

$$\lambda := \frac{(q_{\ell} + t_g)\ell_g}{g} > 0, \ \rho_g := \frac{\ell_g}{z} > 0 \text{ and } \rho_p := \frac{c_p p}{z} > 0.$$

The system of equation (26') - (31') is solved in the appendix 2. It turns out that increasing the tax on pesticides reduces the use of pesticides unambiguously. As could also be expected, raising the subsidy on farm labor input $(\hat{t}_g > 0; t_g < 0)$ results in increasing that input.

The comparative statics is summarized in table 1. The first and second lines show the directions of change if the payroll subsidy and the tax on pesticides, respectively, are changed in isolation. The last line refers to an equal percentage increase of both the tax and the subsidy. Table 1 shows that under mild restrictions spelled out in the appendix $\hat{t}_g > 0$ and/or $\hat{t}_p > 0$ imply $\hat{p} < 0$ and $\hat{\ell}_g > 0$. In view of (14) the sign of \hat{g} is indeterminate since $\hat{\ell}_g > 0$ tends to increase, but $\hat{p} < 0$ tends to decrease the grain energy, but the separate and joint effect of taxes on mice and buzzards is unambiguously positive under the mild restrictions mentioned above.

response	\hat{p}	$\hat{\ell}_g$	ĝ	ĥ	\hat{b}	\hat{q}_ℓ
\hat{t}_g	– a)	+	?	+	+	+
\hat{t}_p	_	+ a)	?	+	+	_
$\hat{t}_g = \hat{t}_p = \hat{t}$	- a)	+ a)	?	+	+	?

a) if σ_D is sufficiently small (see appendix)

Table 1: Tax incidence

¹² Since Pareto efficiency requires $t_g < \theta$ and $t_p > \theta$, $\hat{t}_g = \hat{t}_p > \theta$ can be interpreted as a move towards efficiency, if the initial situation is characterized by $\left|t_g\right| < \left|t_g^*\right|$ and $t_p < t_p^*$.

Proposition 4: Consider the competitive market economy in the absence of any taxes and subsidies and compare the pertaining allocation with the efficient allocation (proposition 3). The no-policy market allocation is characterized

- by excessive use of pesticides
- by too little labor input in farming,
- and by too small populations of mice and buzzards.

Grain may be above or below its efficient level.

Figure 3 illustrates these results using the graph of the functions (14) that had already been employed in figure 1. The letters with subscript o represent the competitive allocation in the absence of taxes and subsidies, and the letters with superscript * refer to the Pareto optimum. It is obvious from figure 3 that the sign of the difference $g^* - g_o$ depends on the relative size of two opposing effects.

Figure 3: Allocative distortions in the market economy

Suppose that $p^* < p_o$ (as assumed above), but $\ell_g^* < \ell_{go}$. Since $\hat{G}_g > 0$, the \hat{G} -line shifts towards the origin. If \hat{G}_g is positive but not too large one would still have $m^* > m_o$ and $b^* > b_o$. However, g^* would be unambiguously smaller than g_o . Hence the qualitative conclusions of the model with regard to the ecosystem are quite robust.

6. Ecosystem dynamics and long-run ecological equilibrium

Up to this section the populations of all species, n_g , n_m and n_b , have been set constant. This was an appropriate assumption for studying the short period but it cannot be maintained, of course, when time is introduced. Denote by n_{vt} for v = g, m, b the populations in period t and let us stick to the simplifying assumption that grain is fully harvested in each period with a constant amount of it being retained for growing grain in the next period. This amounts to

assuming $n_{gt} \equiv \overline{n}_g > 0$ for all t. Hence it is only the populations of mice and buzzards that may change in time.

The next step is to relate equilibrium net energies m_t and b_t to populations. To do that denote by μ and β the constant average net energy stored in each organism of mice and buzzards, respectively. Clearly, m_t/μ and b_t/β is the reproduction rate, i. e. the average net number of new organisms bred in period t by each mouse or buzzard existing in period t. For example, $m_t/\mu = 2.34$ means that each mouse living in period t has, on average, 2.34 descendents (which are assumed to be grown up at the end of period t). On the other hand, $m_t/\mu = -0.16$ is to be interpreted as a situation were the average mouse has no descendents and a 16% chance to be become a prey. Hence at the beginning of period t+1 the populations of mice and buzzards are

$$n_{m,t+1} := \left(\frac{m_t}{\mu} + I\right) n_{mt} \quad \text{and} \quad n_{b,t+1} := \left(\frac{b_t}{\beta} + I\right) n_{bt}$$

$$(32)$$

implying the population growth rates

$$\frac{n_{m,t+1} - n_{mt}}{n_{mt}} = \frac{m_t}{\mu} \quad \text{and} \quad \frac{n_{b,t+1} - n_{bt}}{n_{bt}} = \frac{b_t}{\beta}.$$
 (33)

Clearly, m_t and b_t in (33) are specified, in principle, by the functions M and B from (15). But at this point, it is necessary to recall that in the short period populations entered the analysis of section 2 in (2), (4) and (6) but were suppressed in the subsequent formal analysis for notational convenience. We now need to reactivate the populations n_{mt} and n_{bt} as determinants of short-run ecological equilibria (maintaining the simplifying assumption $n_{gt} = \overline{n}_g >$ for all t) because in the long term these populations are endogenous variables. In other words we simply observe that the functions G, M and B from (15) also depend on populations. Combining (33) with (15) yields the ecosystem dynamics

$$g_t = G(\ell_b, \ell_g, p, s, n_{mt}, n_{bt})$$
(34a)

$$\frac{n_{m,t_n} - n_{mt}}{n_{mt}} = \frac{M(\ell_b, \ell_g, p, s, n_{mt}, n_{bt})}{\mu}$$
(34b)

$$\frac{n_{b,t_n} - n_{bt}}{n_{bt}} = \frac{B(\ell_b, \ell_g, p, n_{mt}, n_{bt})}{\beta}$$
 (34c)

It is beyond the scope of the present paper to investigate the time path of the populations as driven by (34) which would require, in particular, to specify more precisely the complex impact of populations on the short-run equilibrium values $G(\cdot)$, $M(\cdot)$, and $B(\cdot)$. We rather content ourselves with noting that if the ecosystem dynamics converge to a steady state - or long-run ecological equilibrium then for given economic activities ℓ_b , ℓ_g , p and s the stationary populations n_m^* and n_b^* are implicitly determined by

$$M(\ell_b, \ell_g, p, s, n_m^*, n_b^*) = B(\ell_b, \ell_g, p, n_m^*, n_b^*) = 0.$$
(35)

7. Concluding remarks

The present paper demonstrates that environmental-economic interdependence can be fruit-fully modeled by linking a (standard) perfectly competitive economy with a full-fledged equilibrium model of the ecosystem. If green preferences are assumed in such a model all human activities that have an impact on the ecosystem create vast positive or negative externalities. As an implication, the concept of efficient farming (and ranching) must be seriously reconsidered in the light of our analysis. An unexpected result is, e. g., that efficiency requires to subsidize farm labor even though this conclusion may not be robust when further ecological opportunity costs of farming are explicitly taken into consideration. Via complex food chains, agriculture has an indirect influence on many species, exemplified by buzzards in our simple model, that are not directly linked to agricultural production. While this insight is by no means novel, the model presented here allows to deal with the ecological information about the relative size of counteracting effects and feedback effects.

Important questions remain unanswered especially about the ecosystem dynamics and the long-run ecological equilibrium. It is desirable in future work to do without the assumption of myopic farmers and consumers since while myopia might be appropriate for maximizing organisms in the ecosystem, it is hard to accept for economic agents in a dynamic environment.

References

Amir, S. (1979), "Economic interpretations of equilibrium concepts in ecological systems", *Journal of Social and Biological Structure* 2, 293-314 Brown, D., and Rothery, P. (1993), *Models in Biology: Mathematics, Statistics and Computing*, Wiley & Sons, Chichester

Crocker, T. D., and Tschirhart, J. (1992), "Ecosystems, externalities, and economies", *Environmental and Resource Economics* 2, 551-567

Eichner, T., and Pethig, R. (20001), Economic approaches to ecosystem analysis, manuscript

Hannon, B. (1976), "Marginal product pricing in the ecosystem", *Journal of Theoretical Biology* 56, 253-267

Murray, J. D. (1993), Mathematical Biology, 2nd. ed., Springer Verlag, Berlin

Stroebele, W. J., and Wacker, H. (1995), "The economics of harvesting predator-prey systems", *Journal of Economics* 61, 65 – 81

Tschirhart, J. (2000), "General equilibrium of an ecosystem", *Journal of Theoretical Biology* 203, 13 - 32

Appendix

Derivation of (12)

We insert r_{ga} from (8) in (6a): $G^o(\cdot) = e_{og}Y^{og}(\ell_g, m, s) - e_gA^g \Big[R^{ga}(y_{gm})\Big]y_{gm} - R^{ga}(y_{gm})$. Differentiation yields $dg = e_{og}Y^{og}_{\ell_g}d\ell_g + e_{og}Y^{og}_{\ell_g}dm + e_{og}Y^{og}_{\ell_g}ds - \Big[(e_gA^g_r + I)R^{ga}_y + e_gA_g\Big]dy_{gm}$. Since $e_gA^g_r + I = 0$ owing to (7a), we obtain

$$g = G^{I}(\ell_{g}, m, s, y_{gm}). \tag{A1}$$

(A1) and y_{gm} from (10) readily imply

Consider next r_{mf} and r_{ma} from (8) in (6b):

$$M^{o}(\cdot) = T(m_{p}, p) \left\{ e_{mg} a_{g} Y^{gm} \left[g, R^{mf} \left(a_{g} \right) \right] - e_{m} A^{m} \left[R^{am} \left(y_{mb} \right) \right] y_{mb} - R^{ma} \left(y_{mb} \right) - R^{mf} \left(a_{g} \right) \right\}.$$

We differentiate this equation totally and take into account that $e_m y_{mb} A_r^m + l = 0$ and $e_m a_g Y_r^{gm} = l$ is implied by (7b). This yields

$$dm = \underbrace{m_p T_p}_{-} dp + T(m_p, p) e_{mg} y_{gm} da_g + T(m_p, p) e_{mg} a_g Y_g^{gm} dg - \theta_{em} a_m dy_{mb} \quad \text{and hence}$$

$$m = M1 \left(a_g, g, p, y_{mb} \right). \tag{A2}$$

In view of (2) and $\theta_p > 0$ we clearly have $T_p = -m_p \delta(m_p) \theta_p < 0$, but the sign of M_a^l and M_g^l depends on the sign of $T(m_p, p)$. Invoking a_g and y_{mb} from (10) transforms (A2) into $m = M^l [\overline{A}^g(g), g, p, \overline{Y}^{mb}(\ell_b, m)]$. Differentiation yields

$$dm = \frac{M_a^l \overline{A}_g^g + M_g^l}{I - M_v^l \overline{Y}_m^{mb}} dg + \frac{M_p^l}{I - M_v^l \overline{Y}_m^{mb}} dp + \frac{M_v^l \overline{Y}_\ell^{mb}}{I - M_v^l \overline{Y}_m^{mb}} d\ell_b.$$
(A3)

The second an third terms on the right side of (A3) are negative. The numerator of the first term is $M_g^l + M_a^l \overline{A}_g^g$. Analogous to (11) $M_g^l = T(m_p, p)e_{mg}a_g Y_g^{gm}$ is the direct effect of grain on mice via its impact on mice preying productivity. On the other hand,

$$M_a^I \overline{A}_g^g = T(m_p, p) e_{mg} y_{gm} \frac{A_r^g R_y^{ga} Y_g^{gm}}{I - A_r^g R_y^{ga} Y_r^{gm} R_a^{mf}}$$

represents the indirect effect of g on m caused by a growing grain population stepping up its defense. It is plausible to assume that the sign of the net effect is always determined by the sign of the direct effect M_g^I . Hence

$$M^{I}\left[\overline{A}^{g}(g), g, p, \overline{Y}^{mb}(\ell_{b}, m)\right] = \hat{M}(g, \ell_{b}, p), \tag{13b}$$

where $\hat{M}_g > 0$ unless $m_p > 0$ and $\theta(p) > 1$. For convenience of exposition we restrict our further investigation to situations where $\hat{M}_g > 0$.

Now we plug a_m from (10) and r_{bf} from (8) into (6c):

$$B^{o}(\cdot) = e_{mb}\overline{A}^{m}(\ell_{b}, m)Y^{mb}\left\{\ell_{b}, m, R^{bf}\left[\overline{A}^{m}(\ell_{b}, m)\right]\right\} - R^{bf}\left[\overline{A}^{m}(\ell_{b}, m)\right].$$

Since $e_{mb}a_mY_r^{mb}=I$ is implied by (7c), differentiation results in

$$db = e_{mb}(y_{mb} \, \overline{A}_{\ell}^{m} + a_{m} \, Y_{\ell}^{mb}) \, d\ell_{b} + e_{mb}(y_{mb} \, \overline{A}_{m}^{m} + a_{m} \, Y_{m}^{mb}) \, dm \,. \tag{A4}$$

For $v = \ell_b$, m, (A4) is symmetric. Y_v^{mb} is the direct and positive effect on buzzard predation productivity while $y_{mb} \overline{A}_v^m < 0$ is the reduction in predation success caused by the mice's defensive response to increases in v. It appears plausible, again, to assume that the positive direct effect overcompensates the indirect effect. Hence

$$B^{o}\left\{\overline{A}^{m}(\ell_{b}, m), \ell_{b}, m, R^{bf}\left[\overline{A}^{m}(\ell_{b}, m)\right] = \hat{B}(\ell_{b}, m).$$

$$(13c)$$

Comparative static analysis of tax incidence

The equations (26') - (31') are solved for \hat{g} , $\hat{\ell}_g$, \hat{q}_ℓ , \hat{p} and \hat{z} . Combine (28'), (29') and (31'):

$$\hat{q}_{\ell} = -\frac{\mu_g}{I - \mu} \hat{t}_g - \frac{\mu_p}{I - \mu} \hat{t}_p. \tag{A5}$$

Insert \hat{q}_{ℓ} from (A5) into (26') and (28'):

$$\hat{g} - \hat{z} = -\frac{\sigma_D \mu_g}{I - \mu} \hat{t}_g - \frac{\sigma_D \mu_p}{I - \mu} \hat{t}_p, \tag{A6}$$

$$\hat{\ell}_g - \hat{p} = \sigma_g \hat{t}_g + \sigma_p \hat{t}_p, \tag{A7}$$

where

$$\sigma_p := \left[t_g (g - q_p p) \theta_p + q_\ell g \mu_p \theta_g \right] / t_g g > 0 \quad \text{and}$$

$$\sigma_g := -q_p \left(p \theta_g + t_g \ell_g \theta_p \right) / g (I - \mu) > 0 .$$

Substitute \hat{g} from (31') and \hat{z} from (30') in (A6):

$$\hat{\ell}_g + \frac{I - \lambda + \rho_p}{\lambda + \rho_g} \hat{p} = \frac{\sigma_D \mu_g}{(I - \mu)(\lambda + \rho_g)} \hat{t}_g - \frac{\sigma_D \mu_p}{(I - \mu)(\lambda + \rho_g)} \hat{t}_p. \tag{A8}$$

Insert $\hat{\ell}_g$ from (A7) into (A8):

$$\hat{p} = \alpha_g \hat{t}_g - \alpha_p \hat{t}_p \,, \tag{A9}$$

where $\alpha_{\gamma} := \frac{\sigma_{\nu}(I-\mu)(\lambda+\rho_g) + \sigma_D\mu_{\nu}}{(I-\mu)(I+\rho_g+\rho_p)}$ for $\nu = g$, p with $\alpha_p > 0$ and α_g indeterminate in

sign. Combine (A7) and (A9):

$$\hat{\ell}_g = (\sigma_g - \alpha_g)\hat{t}_g + (\sigma_p - \alpha_p)\hat{t}_p \tag{A10}$$

Finally, insert (A9) and (A10) in (30') and (31'):

$$\hat{z} = p_g \left[a_g \left(l + \rho_p \right) - \sigma_g \right] \hat{t}_g + \rho_g \left[\alpha_p \left(l + \rho_p \right) - \sigma_p \right] \hat{t}_p, \tag{A11}$$

$$\hat{g} = (\lambda \sigma_g - \alpha_g)\hat{t}_g + (\lambda \sigma_p - \alpha_p)\hat{t}_p. \tag{A12}$$

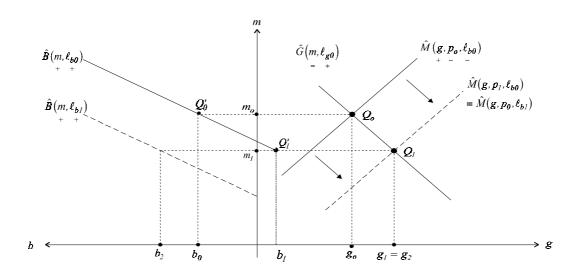


Figure 1: Short-run ecological equilibrium

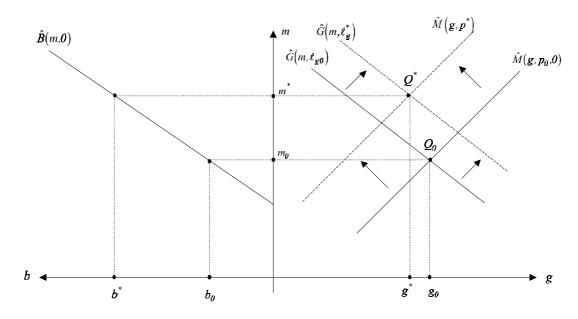


Figure 3: Allocative distortions of the market economy

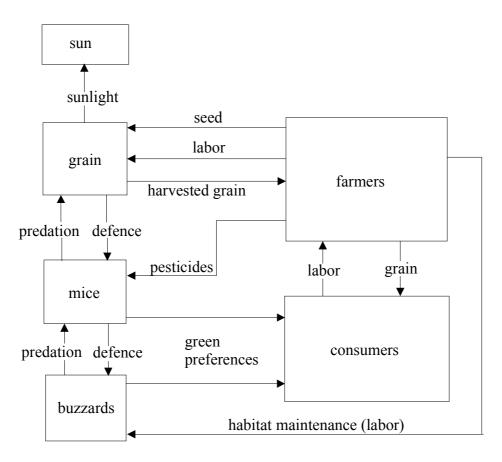


Figure 2: Integrated ecosystem-economy model