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Agriculture, pesticides and the ecosystem

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Abstract

Economists have a good understanding of intra-economic interdependence and a mature methodology of modelling it. Ecologists focus on the complex and sensitive interactions of species in ecosystems. This paper's objective is to suggest a new micro-foundation of ecosystem analysis based on economic methodology, to integrate the analyses of the ecosystem and the economy and focus on the interface of ecosystem–economy relations. Agriculture forms a major part of this interface. The basic assumption is that in the short run the individual organisms of all species behave as if they optimise their costly offensive and defensive activities given other organisms' activities (Nash-behaviour).

We consider an ecosystem with three species in a unidirectional food chain: buzzards feed on mice, mice feed on grain, and grain feeds on solar energy. A fourth species, humans, also feeds on grain. Humans intervene in the ecosystem in various ways. They can grow grain by using seed, farm labour, pesticides and possibly nature conservation measures to maintain buzzard habitat. Short-run ecosystem equilibrium is characterised, and it is shown, in particular, how this equilibrium depends on farming activities. We then link this ecosystem model to a simple model of an agricultural economy. Both systems are solved for equilibrium simultaneously. From an economic perspective the ecosystem induces positive and negative externalities in agricultural production and in consumer 'green' preferences.

The inefficiencies of the competitive economy are identified and some possibilities to restore efficiency through corrective taxes or subsidies are briefly discussed. We also outline how short-run equilibria are connected through ecosystem stock-flow relationships. Due to the complexity of the inter-temporal analysis, the resulting ecosystem dynamics cannot be characterised in general analytical terms. It is a topic for future research to study the dynamics in numerical analysis to understand under which conditions the joint ecological and economic system is driven toward a (sustainable) steady state.

JEL classification: Q10; Q18; Q20; Q28

Keywords: Ecological agriculture; Ecosystem modelling; Nature conservation; Pesticides

1. Introduction

As is well understood, agriculture operates at an important interface between ecological and economic systems. These systems are interdependent and are both characterised by dynamic stock-flow relationships. In ecosystem analysis the latter are often studied in dynamic multi-species models. Macro approaches are applied that take populations as basic endogenous variables and hence disregard the micro structure of intra-ecosystem transactions.[1] On

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[1] This type of modelling is surveyed by Murray (1993) and Brown and Rothery (1993).

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the other hand, economic theory provides valuable insights into the nature of intra-economy interdependence and has developed a mature and powerful methodology of modelling it. Moreover, the explanation of economic growth or decline is based on the methodological concept of moving (short-run or instantaneous) equilibria.[2] In the short run, all flow variables are determined for a set of given stocks and these (equilibrium) flows determine, in turn, the stock adjustments and hence the adjusted set of stocks taken as given in the next short period. The dynamics of the economic system are thus modelled through a sequence of short-run general equilibria.

When it became evident that economic activities had detrimental effects on ecological systems (*ecosystems*, for short), environmental economics developed as a branch of externality theory which, however, often focuses on environment–economy interactions in a rudimentary way. Ecological population models also address the impact of economic activities on ecosystems but anthropogenic distortions enter such analyses often as exogenous parameter shocks only. It appears, therefore, that in their studies of environment–economy interactions, both ecology and economics are biased, but in opposite directions: ecologists tend to disregard the complexity of the economic system, and economists tend to neglect that of the ecosystem.

In our view, environment–economy interdependence cannot be satisfactorily studied unless both intra-economy and intra-ecosystem interdependence is explicitly modelled and unless repercussions set off in one system by disturbances in the other are captured—including the feedback of these repercussions to the system where the disturbance originated.

The present paper aims at developing an integrated general equilibrium model of the economy and the ecosystem. The economy is basically represented by its agricultural sector and the ecosystem is modelled by applying economic methodology[3] with an emphasis on its microfoundation following, to some extent, Hannon (1976), Crocker and Tschirhart (1992), Tschirhart (2000, 2002), Finnoff and Tschirhart (2002) and Pethig and Tschirhart (2002). Our principal objective is to offer a formal analysis of ecosystem–economy interdependence and of the foundations of ecosystem dynamics based on the methodological concept of moving equilibria referred to above. The main focus is on the ecosystem submodel of the short period, since it is the short-run equilibrium allocations that completely determine the inter-temporal stock-flow relations.

The model of the short period is based on the concept of optimising behaviour of individual organisms which has a long tradition in evolutionary ecology (Houston and McNamara, 1999). Mangel and Clark (1988) suggest that foraging individuals optimise a rate of energy return in search for food and that they find out the best way to trade off the rewards with the costs and the risks. Yet to our knowledge, there is no ecological theory that is based on optimising behaviour of organisms and that aims, at the same time, at explaining intra-ecosystem interactions.[4] Like Tschirhart and others (cited above), we assume that the representative organism of each species maximises its net energy—or behaves as if it does so. However, our approach differs substantially from that of Hannon, Crocker and Tschirhart in how the organisms' 'production functions' (physiological functions) are specified and in the concept of short-run ecological equilibrium. Tschirhart (2000) envisages price taking organisms whose demand for prey biomass reacts to relative prices and whose supply of own biomass to its predators is determined by its demand for prey biomass (rationalised by a predation risk argument). In his model, a short-run equilibrium is then reached through a set of prices at which total demand and supply match for the biomass of each and every species.

In the present paper, the optimising organism is modelled in a distinctly different way. Preying as well as avoiding to be preyed are costly activities (where cost takes the form of losing own biomass) which gives rise to optimising behaviour on both the offensive and defensive side given the other organisms'

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[2] The pertinent prototype model is the neoclassical growth model in which all flow variables including investment are determined in short-run general equilibria and where investment is added to the capital stock in the next period.

[3] For a survey and critical assessment of economic approaches to ecosystem analysis, see Eichner and Pethig (2002).

[4] In recent years, the so-called individual-based approach to ecosystems linking heterogeneous individual organisms to community structure has been advanced in the ecological literature. But this literature does not build on optimising behaviour (DeAngelis and Gross, 1992).

strategies (Nash behaviour). The solution concept for the implied game is the Cournot–Nash equilibrium. Unlike Tschirhart and others we do not use equilibrating prices.

To outline the methodology to be suggested here we develop a three-species model of an ecosystem and link that model 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.[5] A fourth species, humans, feeds on grain, too. Humans are able to intervene in the ecosystem in three different ways. They can foster the growth (and harvest) of grain by farm labour input; they can use pesticides to diminish the mice population so that mice leave more grain for harvesting; and they can use resources for buzzard habitat maintenance (nature conservation)—with the consequence that buzzards take more mice. Particular attention will be placed on the derivation of a short-run ecological equilibrium contingent on given levels of economic activities. We then integrate a model of the economy into the ecosystem model with a special focus on the interface of ecosystem–economy interdependence. Both systems are required to settle for equilibrium simultaneously. From the economist’s perspective, the ecosystem creates positive and negative externalities (Crocker and Tschirhart, 1992) emerging in agricultural production and in consumer preferences for the ecosystem (green preferences).

All these investigations aim at clarifying how the flow variables of the ecosystem and their interactions with agricultural activities are determined in the short term. As explained above, the flow variables associated with short-run equilibria determine the adjustment of population stocks such that the analysis of the short run is the key to the dynamics of the ecosystem. This connection between short-run analysis and stock-flow dynamics is then worked out at the conceptual level. The differential population functions we come up with in the present paper are derived from more basic assumptions, i.e. they are micro-founded while such functions are assumed ad hoc in conventional ecological population models of the Lotka–Volterra type. To reveal the specific properties of the differential population equations derived here one would need to elaborate a parametric or even numerical version of our model which is, however, beyond the scope of the present paper.[6]

Section 2 of the paper elaborates on ecological interdependence as well as on the concept and properties of short-run ecological equilibrium. Section 3 combines the ecosystem model with a model of the economy and characterises the efficient allocation. Section 4 discusses the inefficiencies of the competitive economy, specifies the types of distortions in the integrated system and briefly investigates some selective policies to restore efficiency through corrective taxes or subsidies. Section 5 introduces stock-flow relationships and elaborates the conceptual links between short-run ecological equilibria and ecosystem dynamics which may or may not drive the ecosystem toward a steady state (long-run ecological equilibrium). Section 6 concludes.

2. Ecological interdependence and short-run ecological equilibrium

To motivate our analysis of short-run ecological interdependence at the micro-level, consider first the standard formal description of population growth,

$$\frac{n_{v,t+1} - n_{vt}}{n_{vt}} := h_{vt}, \quad v = 1, \ldots, \bar{v}. \tag{1}$$

With n_{vt} denoting the population of species v in period t, Eq. (1) gives us the rate of population growth in period t. Ecological population models specify the growth rate of species v in period t, h_{vt}, to be dependent on its own population in period t, on the populations of some other species and on some vector, λ, of parameters:

$$h_{vt} = H^{vt}(n_{1t}, \ldots, n_{\bar{v}t}, \lambda). \tag{2}$$

In population ecology, predator–prey relationships among species, or mutualism, are then expressed by the signs of the partials of function H^{vt} with respect to populations. More generally, the functional form

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[5] 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.

[6] Numerical dynamic analyses based on the methodology of moving short-run equilibria but relating to grossly different setups are carried out in Tschirhart (2000, 2002), Finnoff and Tschirhart (2002) and Pethig and Tschirhart (2002).

of H^{vt} is chosen to reflect more or less well founded empirical hypotheses, but the form is ad hoc in the sense that it does not emerge as an implication of more basic hypotheses in the formal model.

In the next sections, we aim at deriving functions of type (2) from species interaction in the short period in which all populations are assumed constant. To keep the exposition simple we envisage an ecosystem of given size (space) and a fixed segment of farm land[7] for growing grain. Postponing inter-temporal issues to Section 5, our focus is now on a short period and on an ecosystem with three species only: buzzards, mice and grain. These species form a unilateral non-circular food chain with buzzards feeding on mice, mice feeding on grain and grain feeding on sunlight. The focus is on representative individual organisms of each species, more specifically, on the *net energy* these organisms are able to acquire during the period under consideration. These net energies are denoted g for grain, m for mice and b for buzzards. The organisms' net energies are, respectively,

$$g = e_{og}x_{og}^{\mathrm{d}} - e_g x_{gm}^{\mathrm{d}} - r_{ga}, \tag{3a}$$

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

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

where e_j is the energy per unit biomass of organism j $(j = g, m)$, $e_j > 0$ and constant, e_{ij} the energy intake of predator j per unit of biomass from prey i, $e_{ij} < 0$ and constant[8], x_{ij}^{d} the biomass of prey i caught by predator j, superscript d stands for demand, r_{if} the offensive or predation effort of predator i in terms of own energy spent, r_{ia} the averting or defensive effort of prey i in terms of own energy spent, p the amount of pesticides applied to grain (fields), and $m_p := (e_{gm}x_{gm} - e_m x_{mb} - r_{mf} - r_{ma})$ is the net energy of m in the absence of pesticides

$$T(m_p, p) := [1 - \delta(m_p)\theta(p)] \quad \text{with}$$

$$\delta(m_p) = \begin{cases} 1, & \text{if } m_p \geq 0, \\ -1, & \text{otherwise.} \end{cases}$$

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 $\theta(p) \geq 0$ with $\theta(p) = 0$ for $p = 0$ and[9] $\theta_p > 0, \theta_{pp} \geq 0$. Note that $T(m_p, p) < 0$ if and only if $m_p > 0$ and $\theta(p) > 1$.

Eq. (3) implicitly assume that all predators' demands for prey biomass prevails.[10] The organisms' need of own energy for maintenance (respiration, metabolism, etc.) is accounted for[11] through the coefficients e_{ij}.

The next step is to determine the biomass of prey i caught by predator j as

$$x_{og}^{\mathrm{d}} = y_{og}, \quad x_{gm}^{\mathrm{d}} = a_g y_{gm} \quad \text{and} \quad x_{mb}^{\mathrm{d}} = a_m y_{mb}, \tag{4}$$

with,[12]

$$a_g = A^g(\underset{-}{n_g}, \underset{+}{n_m}, \underset{-}{r_{ga}}), a_m = A^m(\underset{-}{n_m}, \underset{+}{n_b}, \underset{-}{r_{ma}}), \tag{5}$$

$$y_{og} = Y^{og}(\underset{+}{\ell_g}, \underset{-}{n_m}, \underset{-}{m}, \underset{+}{s}),$$
$$y_{gm} = Y^{gm}(\underset{+}{g}, \underset{+}{n_g}, \underset{-}{n_m}, \underset{+}{r_{mf}}),$$
$$y_{mb} = Y^{mb}(\underset{+}{k}, \underset{+}{m}, \underset{+}{n_m}, \underset{-}{n_b}, \underset{+}{r_{bf}}), \tag{6}$$

where $A^v(\cdot) \in]0, 1]$ with $A^v(0) = 1$, and $A_{rr}^v > 0$. The basic idea behind Eqs. (4)–(6) is that a prey can reduce the term a by stepping up its averting effort (r_a) while the predator can enlarge the term y and hence its catch of prey biomass, ceteris paribus, by increasing its offensive effort (r_f). Hence, the prey biomass taken by

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[7] In a more encompassing approach one would treat as endogenous the space devoted to growing grain at the expense of the space available for the ecosystem (proper). See also the remarks following Proposition 1.

[8] In case of $i = 0$ and $j = g$, the intake is not biomass, of course, but solar energy.

[9] Upper case letters represent functions. Subscripts to upper case letters denote partial derivatives.

[10] This assumption is plausible, in our view. Consistency requires to ensure that the intake of prey biomass of all predator organisms equals the outflow of own biomass from all organisms of the prey species. For more details, see Appendix A.

[11] Another way of accounting for maintenance is outlined in Appendix A.

[12] A minus or plus underneath an argument of a function indicates the sign of the pertinent partial derivative. Most hypotheses expressed by the signs of partial derivatives in (5) and (6) are presumably not controversial. But other specifications are conceivable and, perhaps, there are good reasons to make the case for dropping some argument or for including another one, especially when this approach is applied in concrete case studies.

a predator is 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 prey on the predators' preying success, x, while y_{og}, y_{gm} and y_{mb} are the variables under control of the respective predators.[13]

The role of populations in (5) and (6) is straightforward. The success of a given averting effort (r_a) is greater, ceteris paribus, the larger the own population—because with increasing own population it is the more likely that the predator catches another organism—and the smaller the predator population—because a predator–prey encounter is then less likely. 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 because the individual predator faces competition from its own kind.

Y^{og} is the farmers' ecological grain growing 'technology'. He combines seeds, s, and farm labour, ℓ_g, to expose the grain to sunlight and to other nutrients such as 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 which is captured in x_{gm} but also in other ways.[14]

$Y^{gm}(\cdot)$ is the grain 'harvested' by the representative mouse if grain refrains from averting behaviour altogether. $Y^{gb}(\cdot)$ depends on the buzzard's hunting effort, on net mouse energy and on human activity, k. We interpret k as a measure of nature conservation benefiting buzzards. Increasing k means improving buzzard habitat maintenance to the effect that buzzards become more successful predators[15], $Y_k^{mb} > 0$.

Since populations are kept constant in the short run, we simplify notation by suppressing all population variables in (5) and (6) in the following analysis, but we will 'reactivate' them in Section 5. Inserting (4)–(6) in (3) yields:

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

$$M^{\mathrm{o}}(a_g, g, p, r_{ma}, r_{mf}, y_{mb}) := T(m_p, p)[e_{gm}a_g Y^{gm}(g, r_{mf}) - e_m A^m(r_{ma})y_{mb} - r_{mf} - r_{ma}] \qquad (7b)$$

$$B^{\mathrm{o}}(a_m, k, m, r_{bf}) := e_{mb}a_m Y^{mb}(k, m, r_{bf}) - r_{bf}. \qquad (7c)$$

There are four 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 defence (a) variables; third, other organisms' net energies; and finally, human activities k, ℓ_g, p and s. The human or economic activities form links from the economy to the ecosystem. They will be kept constant in the present section but endogenised later and then complemented by links from the ecosystem to the economy.

Recall from (6) that the net energies g or m influence some predator's productivity of hunting. It is plausible to assume that predators take these variables as given, i.e. that they ignore their indirect effect on the net energy of other species. We also assume that each prey takes as given the offensive activities of its predators, and that each predator takes as given the averting activity of its prey. As a consequence, the only variables each organism controls are its own offensive and/or defensive efforts. The principal behavioural assumption is that each organism chooses its efforts *as if it maximises its own net energy*—given all other organisms' offensive and/or defensive activities.

There is a long tradition in ecology to link the evolution of species to optimising behaviour (Houston and McNamara, 1999), and even maximising offspring is an often employed behavioural assumption. The notion that organisms behave as if they maximise their net energy is in line with Hannon (1976), Crocker and Tschirhart (1992), Tschirhart (2000) and others.

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[13] For example, if m does not undertake any averting effort ($r_{ma} = 0$), then $a_m = 1$ and $x^{\mathrm{d}}_{mb} = y_{mb}$. Therefore, y_{mb} is the buzzard's intake of mice biomass in the absence of defensive activities by mice. If, however, $r_{ma} > 0$, then $a_m < 1$ and the buzzards' intake of mice biomass is $x^{\mathrm{d}}_{mb} < y_{mb}$.

[14] Mice is probably not a convincing example of an animal species doing harm to plants independent of and/or 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 setting $Y_m^{\mathrm{og}} = Y_{n_m}^{\mathrm{og}} = 0$.

[15] We could have modelled the impact of k on buzzards similar as the impact of pesticides on mice—except with opposite sign. Rather than claiming empirical evidence for our procedure the main point we want to make is that human activities can affect the ecosystem in various ways.

Table 1
Players and their strategies in the ecosystem game

Organism	Strategy
Grain	a_g
Mice	a_m, y_{gm}
Buzzards	y_{mb}

But while these authors model organisms as price takers, the present model assumes Nash behaviour in the absence of prices. In other words, we conceive of ecosystem interaction as a non-co-operative game between the representative organisms of grain, mice and buzzards.[16] The players and their strategies are listed in Table 1.

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

$$\max_{r_{ga}} G^{o}(\ell_g, r_{ga}, y_{gm}),$$
$$\max_{r_{ma}, r_{mf}} M^{o}(a_g, g, p, r_{ma}, r_{mf}, y_{mb}),$$
$$\max_{r_{bf}} B^{o}(a_m, k, m, r_{bf}).$$

Assuming that the functions G^o, M^o and B^o are strictly concave in r_{ga}, (r_{ma}, r_{mg}) and r_{bf}, respectively, the maximisers are determined as functions,

$$r_{ga} = R^{ga}(\underset{+}{y_{gm}}), \qquad r_{ma} = R^{ma}(\underset{+}{y_{mb}}),$$
$$r_{mf} = R^{mf}(\underset{+}{a_g}), \qquad r_{bf} = R^{bf}(\underset{+}{a_m}). \tag{8}$$

We insert the optimal efforts (8) into (5) and (6) to obtain the best responses,

$$a_g = A^g[R^{ga}(y_{gm})],$$
$$y_{gm} = Y^{gm}[g, R^{mf}(a_g)], \tag{9a}$$

$$a_m = A^m[R^{ma}(y_{mb})],$$
$$y_{mb} = Y^{mb}[k, m, R^{bf}(a_m)]. \tag{9b}$$

Since our model describes a unilateral food chain, it is not surprising that the game disintegrates into two subgames specified in (9a) and (9b). A Nash equilibrium of these subgames consists of strategies (a_g^*, y_{gm}^*) and (a_m^*, y_{mb}^*) determined by solving the two equations in (9a) and (9b), respectively. Total differentiation reveals that there are (equilibrium) functions $\bar{A}^g$, $\bar{A}^m$, $\bar{Y}^{gm}$ and $\bar{Y}^{mb}$ such that,

$$a_g^* = \bar{A}^g(\underset{-}{g}), \qquad y_{gm}^* = \bar{Y}^{gm}(\underset{+}{g}),$$
$$a_m^* = \bar{A}^m(\underset{-}{k}, \underset{-}{m}), \qquad y_{mb}^* = \bar{Y}^{mb}(\underset{+}{k}, \underset{+}{m}). \tag{10}$$

The signs of the partial derivatives in (10) are unambiguous except for $\bar{Y}_g^{gm} > 0$ and $\bar{Y}_m^{mb} > 0$. To see this, consider y^{gm} from (9a) and a_g^* from (10) to write: $y_{gm} = \bar{Y}^{gm}(g) = Y^{gm}\{g, R^{mf}[\bar{A}^g(g)]\}$. Total differentiation yields, after some rearrangement of terms,

$$Y_g^{gm} = \underset{+}{Y_g^{gm}} + \underset{+}{Y_r^{gm}}\,\underset{+}{R_a^{mf}}\,\underset{-}{\bar{A}_g^g} \tag{11}$$

To interpret (11) suppose the net energy of grain is increased. Then grain steps up its defensive effort ($\bar{A}_g^g < 0$) which has a negative but indirect effect on mice predation productivity. On the other hand, due to $Y_g^{gm} > 0$ from (6), increasing grain energy has a direct positive effect on mice predation. We consider it plausible that the positive direct effect overcompensates the negative indirect effect.[17]

We proceed to determine the equilibrium net energies by combining (7) with (8) and (10):

$$g = G^o\{\ell_g, R^{ga}[\bar{Y}^{gm}(g)], \bar{Y}^{gm}(g)\}, \tag{12a}$$

$$m = M^o\{g, p, R^{ma}[\bar{Y}^{mb}(k, m)],$$
$$R^{mf}[\bar{A}^g(g)], \bar{Y}^{mb}(k, m)\}, \tag{12b}$$

$$b = B^o\{\bar{A}^m(k, m), k, m, R^{bf}[\bar{A}^m(k, m)]\}. \tag{12c}$$

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[16] A game in normal form requires to specify the players, their strategies and their payoff functions which map strategy profiles into payoffs. In the game under consideration, players and their strategies are well defined and payoffs are net energies. But note that the Eq. (7) do not represent standard payoff functions since the domains of G^o, M^o and B^o contain the payoffs of other players, among other variables.

[17] The capacity of plants to discourage their predators from feeding on them is small, if not zero. We introduced the assumption $A_r^g < 0$ primarily to demonstrate the generic structure of the food chain model. $\bar{Y}_m^{mb}$ is given by an expression analogous to (11). In contrast to grain, averting behaviour of mice is certainly empirically significant. We find it (again) realistic that the indirect effect is of second order only, and we will therefore base our subsequent interpretations on this assumption. Note, however, that this is done mainly for the convenience of avoiding the tedious discussion of several alternative scenarios. Determining the sigh of the net effect is ultimately an empirical issue which cannot be settled here.

The net energies (g, m, b) satisfying (12) constitute a *short-run ecosystem equilibrium*. In what follows we transform (12) in order to determine each equilibrium net energy as a function of the economic activities (k, ℓ_g, p, s), and to specify, at the same time, how the equilibrium net energies respond to exogenous changes of economic activities. It is convenient to proceed in two steps: First we transform each equation in (12) such that the respective species' net energy no longer appears on both sides of the equation. As shown in Appendix B, the system of Eq. (12) is equivalent to:

$$g = \hat{G}(\underset{+}{\ell_g}, \underset{-}{m}, \underset{+}{s}) \tag{13a}$$

$$m = \hat{M}(\underset{+}{g}, \underset{-}{k}, \underset{-}{p}), \tag{13b}$$

$$b = \hat{B}(\underset{+}{k}, \underset{+}{m}). \tag{13c}$$

The signs of the partials in (13) are clear-cut except for $\hat{M}_g$, $\hat{B}_k$ and $\hat{B}_m$. The signs assigned to the three partials in (13) result from assuming that offensive activities respond more strongly to the variables g, k and m, respectively, than defensive variables. $\hat{M}_g > 0$ presupposes, in addition, $\theta(p) \leq 1$ in case of $m_p > 0$. More details are presented in Appendix B.

It remains to determine the reduced form of (13). For that purpose, we differentiate (13b) and (13c) to obtain:

$$\mathrm{d}g = \frac{1}{1 - \hat{G}_{m-}\hat{M}_{g+}} \times [\underset{+}{\hat{G}_{\ell_g}}\,\mathrm{d}\ell_g + \underset{-}{\hat{G}_m}\,\underset{-}{\hat{M}_k}\,\mathrm{d}k + \underset{-}{\hat{G}_m}\,\underset{-}{\hat{M}_p}\,\mathrm{d}p],$$

$$\mathrm{d}m = \frac{1}{1 - \hat{G}_{m-}\hat{M}_{g+}} \times [\underset{+}{\hat{M}_g}\,\underset{+}{\hat{G}_{\ell_g}}\,\mathrm{d}\ell_g + \underset{-}{\hat{M}_k}\,\mathrm{d}k + \underset{-}{\hat{M}_p}\,\mathrm{d}p].$$

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

$$g = G(\underset{+}{k}, \underset{+}{\ell_g}, \underset{+}{p}, \underset{+}{s}) := \hat{G}[\ell_g, \hat{M}(g, k, p), s], \tag{14a}$$

$$m = M(\underset{+}{k}, \underset{-}{\ell_g}, \underset{-}{p}, \underset{+}{s}) := \hat{M}[\hat{G}(\ell_g, m, s), k, p]. \tag{14b}$$

Finally, we combine (13a) and (14b) to obtain,

$$b = B(\underset{+}{k}, \underset{-}{\ell_g}, \underset{-}{p}, \underset{+}{s}) := \hat{B}[k, M(k, \ell_g, p, s)]. \tag{14c}$$

In (14c), we have $\partial B/\partial k := B_k = \hat{B}_k + \hat{B}_m M_k$. By setting $B_k > 0$ we assume (again) that the positive direct effect of buzzard habitat maintenance dominates the negative indirect effect.

The short-run ecosystem equilibrium and the impact of 'shocks' from the economic system on that equilibrium can be conveniently illustrated by recurring to the functions $\hat{G}$, $\hat{M}$ and $\hat{B}$ from (13). In Fig. 1, (b_0, g_0, m_0) is the solution to (13) for given $k = k_0$, $\ell_g = \ell_{g0}$, $p = p_0$ and $s = s_0$.

Fig. 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 hurts not only mice but also buzzards: the net energy of organism m shrinks from m_0 to m_1 and that of organism b shrinks from b_0 to b_1. The shift from Q_0 to Q_1 leaves the representative mouse with reduced but still positive net energy whereas the net energy of the representative buzzard becomes negative ($b_1 < 0$).[18] Note also that the additional use of pesticides increases grain net energy.[19]

Another interesting comparative static result is obtained as follows: We start again with an initial equilibrium for a given vector (What is missing here?) given $(k_0, \ell_{g0}, p_0, s_0)$. But now we leave ℓ_{g0} and p_0 unchanged and improve, instead, nature conservation from k_0 to $k_1 > k_0$. In Fig. 1, k_1 has been chosen for simplicity such that the new $\hat{M}$-curve intersects the $\hat{G}$-curve in Q_1 (as before, when p rather than k was increased). Hence, the impact on grain is the same as in case of increasing p, but the buzzard net energy is still positive. In Fig. 1, it even increases[20] from b_0 to b_2. Our model thus demonstrates that farmers have

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[18] As will be shown in Section 5, $b_1 < 0$ translates into a declining buzzard population.

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

[20] Recall, however, from (14c) that $B_k > 0$ requires the direct effect of k on $\hat{B}$ to dominate the indirect effect $\hat{B}_m\hat{M}_k$. To illustrate the alternative case, $B_k < 0$, in Fig. 1 assume that the dashed line representing function $\hat{B}(m, k_1)$ is drawn sufficiently close to but still below the solid line depicting the graph of $\hat{B}(m, k_0)$. Then we would have $b_2 < b_0$, hence $B_k < 0$.

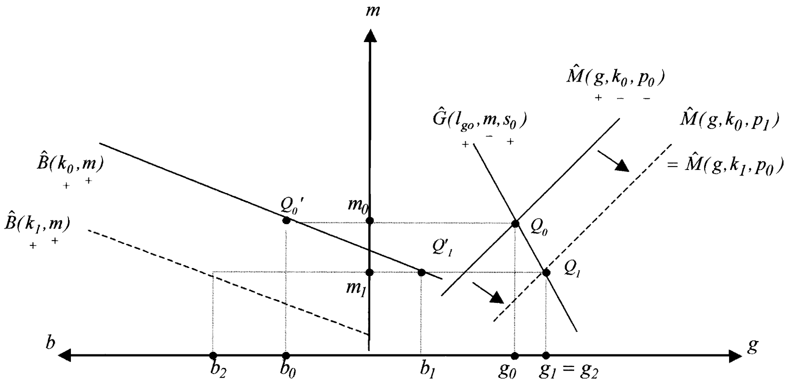

Fig. 1. Short-run ecological equilibrium.

at their disposal two different strategies for enhancing farming productivity: fighting against nature (pesticides) or collaborating with nature (buzzard habitat maintenance). Provided that farmers are able and/or willing to take both options into account (which cannot be taken for granted; see below) their choice will depend on comparative costs.

In view of (14), our results on short-run ecological equilibrium and its properties are now summarised in the following proposition.

Proposition 1.

(i) *For any given economic activities* (k, 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 labour input* (ℓ_g) *and grain seed (s) benefits all species*;
  - *nature conservation* (*support for buzzards*) (k) *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.*

It conforms to our intuition that all farming activities, k, ℓ_g, p and s boost the growth of grain, but it is less intuitive that in (14b) and (14c) farm labour and seed also foster mice and buzzards. In the real world, farming may reduce and/or deteriorate the habitat of mice and buzzards. If that observation were included in our formal model, farm labour and seed would turn out to be less beneficial to the ecosystem.

3. Efficient farming in the integrated ecosystem–economy model

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

The purpose of grain farming is to harvest the entire grain biomass for (human) consumption.[21] Hence function G in (14a) represents the *production function for grain*. To ease the exposition we assume that a constant amount of harvested grain is set aside in each period to be used as seed for growing grain in the next period: $s = \bar{s}$.[22] Pesticides and nature conservation are assumed be produced with labour input ℓ_p and ℓ_k, respectively, according to the linear functions:

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[21] For simplicity we dispense with modelling grain as an intermediate good to be transformed into final consumer goods say ‘bread’.

[22] In a more encompassing approach, the amount of seed to be retained would be included in the social planer’s or the farmers’ intertemporal optimisation calculus.

$$\ell_p = c_p p \quad \text{and}$$

$$\ell_k = c_k k \quad (c_p, c_k > 0 \text{ and constant}) \tag{15}$$

There are n_c consumers with utility,

$$u_i = U^i(\underset{+}{b}, \underset{+}{g_i}, \underset{-}{\ell_i}, \underset{+}{m}, \underset{+}{n_b}, \underset{+}{n_m}), \quad i = 1, \ldots, n_c, \tag{16}$$

where ℓ_i is consumer i's endogenous labour supply and g_i is his or her consumption of grain. The individual consumer considers the net energies of mice and buzzards as given. But he or she needs not be indifferent with respect to the state of the ecosystem as represented by g, m, n_b and n_m. It is conceivable that for $v = m, b, n_b, n_m$ the marginal utility U_v^i is zero, positive or negative. We will focus on *green preferences*, defined by $U_v^i > 0$ for $v = m, b, n_b, n_m$ and compare this scenario with one in which consumers do not care about the ecosystem: $U_v^i = 0$ for $v = m, b, n_b, n_m$. It should be emphasised, however, that the consumers' positive evaluation of mice and buzzards is not meant to reflect just the esthetics of wildlife as a matter of personal taste but rather relates to important services of nature for human health, recreation, biodiversity benefits, etc.

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

$$\sum_{i=1}^{n_c} \ell_i \geq \ell_g + \ell_k + \ell_p. \tag{17}$$

We restrict our exposition to the case of identical consumers. With this simplification we invoke (14), (15) and (17) to rewrite (16):

$$u = U\left[B(k, \ell_g, p, \bar{s}), \frac{G(k, \ell_g, p, \bar{s}) - g(\bar{s})}{n_c}, \frac{\ell_g + c_k k + c_p p}{n_c}, M(k, \ell_g, p, \bar{s}), n_b, n_m\right],$$

where $g(\bar{s})$ is the grain energy needed for retaining the quantity $\bar{s}$ of grain seed to be used in the next period. To characterise an efficient allocation we maximise U with respect to k, ℓ_g and p. Assuming that the functions G, M and B are concave, an interior solution is characterised by the first order conditions:[23]

$$\underset{+}{G_k} + n_c W_{mg} \underset{-}{M_k} + n_c W_{bg} \underset{+}{B_k} = -\underset{-}{W_{\ell g}}, \tag{18a}$$

$$\underset{+}{G_{\ell g}} + n_c W_{mg} \underset{+}{M_{\ell_g}} + n_c W_{bg} \underset{+}{B_{\ell_g}} = -c_k \underset{-}{W_{\ell g}}, \tag{18b}$$

$$\underset{+}{G_p} + n_c W_{mg} \underset{-}{M_p} + n_c W_{bg} \underset{-}{B_p} = -c_p \underset{-}{W_{\ell g}}, \tag{18c}$$

where $W_{vg} := U_v/U_g$ for $v = b, \ell, m$ is the marginal willingness to pay for V in terms of grain. In (18), the terms $n_c W_{mg} M_v$ and $n_c W_{bg} B_v$ for $v = k, \ell_g, p$ are aggregate marginal values consumers attach to the economic activity v for its impact on mice and buzzards, respectively. These terms are summation conditions as in Samuelson's well-known rule for the efficient allocation of pure public goods. Hence, (18) demonstrates that for an allocation of the economic activities k, ℓ_g and p to be efficient it is necessary to consider not only their direct productivity effect but also to account for the indirect marginal benefits and costs generated by these economic activities through their impact on the ecosystem. In view of this interpretation, the left sides of (18) represent total direct and indirect (net) benefits of activity v and the right sides show marginal labour costs (all in terms of grain). The information (18) is summarised in the following proposition.

Proposition 2.

(i) *Suppose consumers are indifferent with respect to the ecosystem* ($W_{mg} = W_{bg} = 0$). *Then it is efficient to use each 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 consumer preferences are green* (W_{mg}, $W_{bg} > 0$).

- *It is not efficient to use pesticides unless their marginal productivity* (*at* $p = 0$) *is sufficiently larger than their marginal production costs to account for their negative side effects on mice and buzzards.*
- *Efficient buzzard habitat maintenance may be at about the same scale as in the case in which*

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[23] Corner solutions are ignored in (18). They may be relevant, however, since it may be optimal in some cases to use no pesticides at all.

consumers do not care about the ecosystem, because its positive effect on buzzards is opposed by a negative side effect on mice. If $W_{bg} > 0$ and $W_{mg} \leq 0$, it may be efficient to foster buzzards, even if marginal productivity G_k at $k = 0$ falls short of marginal labour cost.

Even though (18) does not allow for a straightforward comparison of allocative efficiency in economies with and without green preferences, its thrust is that the greening of preferences leads to increased farming, reduced use of pesticides and an ambiguous change in buzzards habitat care.

4. Competitive markets and taxes

We envisage a perfectly competitive economy with markets for pesticides, grain and labour, and we denote market prices by $q := (q_k, q_\ell, q_p)$. There is no market for nature conservation. As in the last section we keep grain seed constant ($s = \bar{s}$) and hence suppress the market for seed altogether. We also introduce taxes $\tau := (\tau_k, \tau_\ell, \tau_p)$ consisting of a tax τ_k on nature conservation, a tax τ_ℓ on farm labour and a tax τ_p on pesticides. Tax rates are not sign-constrained and, hence, may turn out to be subsidies.

Recall that the production function for grain G from (14a) implicitly captures all ecological interactions relevant for farming. It was appropriate to employ this function to characterise allocative efficiency in the previous section, but in a decentralised market economy farmers may ignore some or all ecosystem interdependence with an impact on farming. To account for incomplete ecosystem information of farmers in a stylised way we distinguish three different types of farmers:[24]

- Farmers who neither use pesticides nor care for buzzard habitat and who take as given the damage mice inflict on their crop are called *ignorant farmers*. They consider $g = \hat{G}(\ell_g, m, \bar{s})$ from (13a) as their relevant grain production function.
- Farmers who know about and take advantage of the productivity enhancing effect of pesticides but who do not care about the buzzard habitat are referred to as *conventional farmers*. These farmers may disregard nature conservation either because they are ignorant about the implied productivity effect or because habitat maintenance is beyond their control due to limited property rights since the grain fields they own are only a small segment of the buzzards' habitat. Conventional farmers take $g = G(k \equiv 0, \ell_g, p, \bar{s})$ from (14a) as their grain production function.
- Farmers who have a full understanding of the grain production function G from (14a) and are also able to take both pesticides and habitat care into account are called *green farmers*. They use the 'correct' production function $g = G(k, \ell_g, p, \bar{s})$ from (14a).

These three types of farmers constitute three different economic scenarios each of which has two sub-scenarios depending on whether consumer preferences are green or not. We will not investigate all these scenarios in detail but it appears worthwhile to offer some discussion of their efficiency properties and comparative performance. To reduce complexity we restrict attention to integrated ecosystem–economy models in which positive values of nature conservation, farm labour and pesticides are efficient (as implied by (18)).

Green farming (*scenario 1*). The grain production function is (14) and hence farmers solve the problem:

$$\underset{(k,\ell_g,p)}{\text{Maximize}}\; q_g G(k, \ell_g, p, \bar{s}) - (q_\ell + \tau_\ell)\ell_g - \left(q_\ell + \frac{\tau_k}{c_k}\right) c_k k - (q_p + \tau_p)p. \tag{19}$$

For an interior solution the first order conditions are,

$$q_k G_k - \tau_k = c_k q_\ell, \qquad q_g G_{\ell_g} - \tau_\ell = q_\ell, \qquad q_p G_p - \tau_p = c_p q_\ell. \tag{20}$$

The representative consumer solves the Lagrange problem,

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[24] We only consider a representative farmer implying that all farmers are treated symmetrically. Therefore, externalities within the farming sector cannot arise—as e.g. the case of buzzards supported by one farmer eating mice on a neighbor's land. Explicitly dealing with such externalities is an important item for future research.

$$L = U\left(b, \frac{g-g(\bar{s})}{n_c}\ell, m, n_b, n_m\right) + \lambda\left(q_\ell \ell + \rho - \frac{g-g(\bar{s})}{n_c}\right), \qquad (21)$$

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

$$-W_{\ell g} = q_\ell. \qquad (22)$$

Now we combine (22) and (20) to compare the result with (18).

Proposition 3. *Consider an economy with green farmers (scenario 1).*

(i) *If consumer preferences are not green (scenario 1a) the competitive market allocation is efficient.*

(ii) *If consumer preferences are green (scenario 1b) the competitive market allocation is efficient, if and only if it is supported by tax/subsidy rates*

$$\tau_k^* = \underset{-}{n_c W_{mg} M_k} + \underset{+}{n_c W_{bg} B_k},$$

$$\tau_\ell^* = \underset{+}{n_c W_{mg} M_{\ell_g}} + \underset{+}{n_c W_{bg} B_{\ell_g}}, \qquad \textit{and}$$

$$\tau_p^* = \underset{-}{n_c W_{mg} M_p} + \underset{-}{n_c W_{bg} B_p}.$$

τ_ℓ^* is a subsidy, τ_p^* is a tax and τ_k^* may be either a subsidy or a tax or zero.

In scenario 1a, the ecosystem depends unilaterally on the economy, and farmers take that linkage fully into account. In contrast, ecosystem disturbances through farming feed back into the economy in case of green preferences (scenario 1b). While the necessity of taxing pesticides was to be expected in the latter scenario, it is less obvious that efficiency requires subsidising farm labour. As observed in the context of Proposition 1, the model appears to overestimate the ecological value of farm labour because it ignores the ecological opportunity costs of growing grain.

Conventional farming (*scenario 2*). We replace the farmers' maximisation problem (19) by Maximize $_{(\ell_g, p)}\, q_g G(k \equiv 0, \ell_g, p, \bar{s}) - (q_\ell + \tau_\ell)\ell_g - (q_p + \tau_p)p$. This yields the FOCs $q_g G_{\ell_g} - \tau_\ell = q_\ell$ and $q_g G_p - \tau_p = c_p q_\ell$, as before, but also implies $q_k G_k - \tau_k > c_k q_\ell$. Owing to the last inequality, conventional farming induces an allocative distortion which is the only cause of inefficiency in scenario 2, if consumer preferences are not green (scenerio 2a). In case of green preferences, the production externality of scenario 2a is augmented by the consumption externalities with regard to mice and buzzards (scenario 2b). Note also that with conventional farmers there does not exist a tax-subsidy scheme $\tau := (\tau_k, \tau_\ell, \tau_p)$ that restores efficiency.[25]

On the other hand, if farmers are not able to care for the buzzards' habitat themselves, ecological education and enlightenment does not help. Instead, some kind of co-operative arrangement between farmers and the owners of the habitat would be necessary to provide for efficient habitat maintenance. In case such co-operation fails or the habitat is made up of public lands and forests, the government is called for to induce or provide appropriate nature conservation services.

Ignorant farming (*scenario 3*). In this case, the farmers' maximisation problem is: *Maximize*$_{(\ell_g)}\, q_g \hat{G}(\ell_g, m, \bar{s}) - (q_\ell + \tau_\ell)\ell_g$. Clearly, growing grain is now severely distorted by two distinct production externalities, since the farmers ignore the impact of both k and p on m. The resultant inefficiency is further aggravated when consumer preferences are green. With the tax on farm labour being the only tax instrument left, efficiency cannot be restored, in general.

Casual observation of modern agriculture shows that farmers have learned to take advantage of the productivity effect of pesticides (and use them excessively, at times). Hence, the underprovision of nature conservation services of scenario 2 may well be a more serious empirical problem than the failure to use pesticides (if and when it is appropriate) in scenario 3.

The preceding discussion is summed up in the following proposition.

Proposition 4. *Consider a general competitive equilibrium in an integrated ecosystem–economy model.*

(i) *Without policy intervention, the equilibrium is efficient if and only if (a) all consumers are indifferent with respect to the state of the ecosystem, (b)*

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[25] The reason is that the solution to (23) subject to $k \equiv 0$ implies $G_k|_{k=0} > q_\ell = -W_{\ell g}$. There is a second-best tax-subsidy scheme (τ_g^o, τ_p^o), but our conjecture is that the quantity of pesticides that obtain, p_o, is greater than the efficient quantity p^*.

farmers have a full understanding of ecosystem interdependence on growing grain and (*c*) *the appropriate level of nature conservation is secured either by the farmers themselves or others* (*e.g. the government*).

(ii) *If one or both of the last two conditions fail to hold, efficiency cannot be restored with the help of taxes or subsidies on farm labour, pesticides and/or nature conservation services.*[26]

If market allocations are inefficient, the comparison of marginal conditions characterising efficiency on the one hand and market distortions on the other hand does not allow for straightforward conclusions about how the inefficient market allocation deviates from the optimum. In particular, we do not know how the net energies of mice and buzzards deviate from their optimum values. Precise answers to these questions would require numerical analysis, which is beyond the scope of this paper. Our conjecture is that in all scenarios (except the efficient scenario 1a) the no-policy market allocation is characterised by excessive use of pesticides, by too little labour input in farming, by insufficient nature conservation and by too small net energies of mice and buzzards. Grain may be above or below its efficient level.

Up to this point, the integrated ecosystem–economy analysis provides a number of interesting insights and results. But since this paper is primarily about the methodology of integrated ecosystem–economy analysis, it is also necessary to spell out more explicitly the logic of the joint short-run equilibrium in both systems. Clearly, in each of the scenarios defined above, *a joint short-run ecosystem–economy equilibrium is constituted by a vector of prices and taxes* (q, τ) *and an allocation* $(g, m, b; k, \ell_g, p, \bar{s})$ *such that*:

- $(k, \ell_g, p, \bar{s})$ *satisfies* (19) *and is technologically feasible*;
- *consumers maximise their utility and producers maximise their profits for given* (q, τ); *and*
- *the equations* $g = G(k, \ell_g, p, \bar{s}), m = M(k, \ell_g, p, \bar{s})$ *and* $b = B(k, \ell_g, p, \bar{s})$ *from* (14) *hold.*

Hence, a joint short-run equilibrium requires: (i) the simultaneous determination of equilibrium in both the ecosystem and the economy and (ii) the equilibrium allocation depends on the economic scenario as well as on the tax rates chosen (if any). To restate observation (ii) in more formal terms we introduce the index $\sigma = $ 1a, 1b, 2a, 2b, 3a, 3b to describe the scenario of the economy under consideration and write the joint equilibrium allocation as:

$$[G^*(\sigma, \tau), M^*(\sigma, \tau), B^*(\sigma, \tau), K^*(\sigma, \tau), L^*(\sigma, \tau), P^*(\sigma, \tau),]$$

where

- $G^*(\sigma, \tau) = G[K^*(\sigma, \tau), L^*(\sigma, \tau), P^*(\sigma, \tau)]$,
- $M^*(\sigma, \tau) = M[K^*(\sigma, \tau), L^*(\sigma, \tau), P^*(\sigma, \tau)]$ and
- $B^*(\sigma, \tau) = B[K^*(\sigma, \tau), L^*(\sigma, \tau), P^*(\sigma, \tau)]$.

5. 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 is an appropriate assumption in the short run but cannot be maintained in the long run. Now we denote the populations in period t by n_{vt} for $v = g, m, b$ and maintain 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 $n_{gt} \equiv n_g(\bar{s}) > 0$ for all t. Hence, only mice and buzzards populations change over time.

The next step is to relate equilibrium net energies m_t and b_t to populations. This is done in a stylised way by assuming that γ, μ and β is the constant average net energy embodied in each organism of grain, mice and buzzards, respectively. Consequently, g_t/γ, m_t/μ and b_t/β is the average number of new organisms bred in period t by each grain, mouse or buzzard existing at the beginning of period t. For example, $m_t/\mu = 2.34$ means that each mouse living in period t has, on average, 2.34 offspring (which are assumed to be grown up at the end of period t). Similarly, $m_t/\mu = -0.16$ is interpreted as a situation were the average mouse has no descendants and a 16% chance not to survive the period. Hence at the beginning of period $t + 1$ the populations are:

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[26] This observation does not imply that other policy instruments could not do the job. But the discussion of alternative instruments is beyond the scope of this paper.

$$n_{g,t+1} := \left(\frac{0}{\gamma}+1\right) n_g(\bar{s}) = n_g(\bar{s}),$$
$$n_{m,t+1} := \left(\frac{m_t}{\mu}+1\right) n_{mt} \quad \text{and}$$
$$n_{b,t+1} := \left(\frac{b_t}{\beta}+1\right) n_{bt}. \tag{24}$$

implying the population growth rates,

$$\frac{n_{g,t+1}-n_{gt}}{n_{gt}} = 0, \qquad \frac{n_{m,t+1}-n_{mt}}{n_{mt}} = \frac{m_t}{\mu} \quad \text{and}$$
$$\frac{n_{b,t+1}-n_{bt}}{n_{bt}} = \frac{b_t}{\beta}. \tag{25}$$

Comparing (25) to (1) and setting $h_{mt} = m_t/\mu$ and $h_{bt} = b_t/\beta$ reveals that our entire previous analysis was directed to provide a foundation for the population growth rates. Clearly, m_t and b_t in (25) are specified by the functions M^* and B^* from (23). But at this point, it is necessary to recall that in the short run, populations entered the analysis of Section 2 in (3), (5), (6) and (16) and were suppressed in the subsequent formal analysis for notational convenience (only). We now need to 'reactivate' the populations $n_t := (n_{gt}, n_{mt}, n_{bt})$ as determinants of short-run ecological equilibrium because in the long run these populations are endogenous. In other words, we observe that the functions G^*, M^* and B^* from (23) also depend on populations:

$$g_t = G^*(n_t, \sigma, \tau_t), \qquad m_t = M^*(n_t, \sigma, \tau_t),$$
$$b_t = B^*(n_t, \sigma, \tau_t). \tag{26}$$

Conceptually, the sign of the derivatives $\partial V^*/\partial n_t$ for $V^* = G^*, M^*, B^*$ from (26) is determined in our short run model (as well as the signs of $\partial V^*/\partial\sigma$ and $\partial V^*/\partial\tau_t$). But due to the complexities of short-run ecosystem–economy interdependence, the net effects of n_t, σ and τ_t on the equilibrium values of net energies cannot be determined without parametric or numerical analysis. In the present paper, we content ourselves with the limited qualitative information condensed in (26) and proceed by combining (25) and (26) to obtain:

$$\frac{n_{m,t+1}-n_{mt}}{n_{mt}} = \frac{M^*(n_t, \sigma, \tau_t)}{\mu},$$
$$\frac{n_{b,t+1}-n_{bt}}{n_{bt}} = \frac{B^*(n_t, \sigma, \tau_t)}{\beta}. \tag{27}$$

Without numerical specification of the functional forms G^*, M^* and B^* it is impossible to characterise the population dynamics (27). We observe, however, that since population growth rates depend on human behaviour, economic activities and on environmental policy, humans have great influence on how the ecosystem develops over time. In the case that, for given values of $\bar{s}$, σ and τ, the ecosystem dynamics converge to a steady state (also called long-run ecological equilibrium), the stationary populations $n^* := [n_g(\bar{s}), n_m^*, n_b^*]$ are implicitly determined by

$$G^*(n^*, \sigma, \tau) > 0 \text{ and const.},$$
$$M^*(n^*, \sigma, \tau) = B^*(n^*, \sigma, \tau) = 0. \tag{28}$$

6. Concluding remarks

We first modelled short-run *intra-ecosystem interdependence* based on species behaviour at the micro level and introduced the concept of short-run ecosystem equilibrium. Then we demonstrated that *ecosystem–economy interdependence* can be fruitfully studied by linking a standard perfectly competitive economy with our short-run equilibrium model of the ecosystem. Owing to the interdependence of both systems, the joint equilibrium must be simultaneously determined. As a result, inter-temporal economic performance depends on how the species populations develop over time. Conversely, the species population dynamics depend on farming styles (ignorant, conventional, green), on consumer valuation of the ecosystem (preferences being green or not) and on ecosystem policies (taxes or subsidies).

If preferences are green, farming and other human activities which have an impact on the ecosystem create positive or negative consumption externalities. A rather unexpected result of green preferences is that subsidising farm labour is efficiency enhancing even though this conclusion may not be robust when the ecological opportunity costs of farming are accounted for. With our main focus on agriculture we showed that, via ecological food chains, agriculture has an indirect influence on some of those species, exemplified by buzzards in our simple model, that are not *directly* linked to farming. Moreover, in the light of our analysis the concept of efficient farming must be reconsidered since farming performance depends on which and/or how many of the farming-related ecosystem interdependencies farmers take into account. While these insights are not entirely novel, we derive them in a formal well-defined model that explicitly deals with relevant ecological interactions and 'shocks' spreading from one system to the other, including feedback effects into the system where they originated.

We emphasised in the introduction that the main contribution of this paper is to suggest a new methodological approach to the analysis of ecosystem–economy interdependence. Hence our principal focus was on the conceptual procedure rather than on substantive results. Even though a number of interesting specific conclusions have been reached, important questions remained unanswered especially about the characteristics of ecosystem dynamics and long-run ecological equilibrium. Among the issues for future research is also the question, under which conditions one would obtain, in the framework suggested here, predator–prey population interactions of the Lotka–Volterra type. In our model, population dynamics with endogenous growth rates can probably only be handled in numerical analysis. As is well known, there is a considerable cost of calibration in terms of loss of algebraic generality. But the upside is that one can add much more realistic structure to the model so that it is no longer allegoric (see footnote 3) but can be applied and/or tested in real-world case studies.

Another possibly controversial issue is whether it is sensible to model all economic and ecological agents as *myopic* maximisers, as we have. Admittedly, assuming maximising within the short-run time horizon is restrictive. Economic agents are forward looking, at least to some extent, and therefore it might be more realistic to conceive of them as inter-temporal maximisers. There is also experimental evidence suggesting that animals apply hyperbolic discounting when considering the future (Ainslie, 1992). It is not so clear to us, however, whether assuming rational expectations and maximising over an infinite time horizon is more realistic than the opposite polar case of myopic short-run maximisation. Anyway, it seems necessary and worthwhile to further follow both lines of modelling which can be done within our framework. The comparison promises to provide additional insights into the important issue of sustainable development and, more specifically, sustainable agriculture.

When environmental and nature conservation policies are at issue, myopia is definitively not an adequate guideline. In our paper, we did not pay adequate attention to such policy issues. We investigated only briefly the potential and limits of welfare improving tax-subsidy schemes applied in the short run (and hence being also myopic), which allowed us to identify such tax policies as a major determinant of population growth rates and hence of ecosystem dynamics, more generally. The few tax policies discussed in the paper only served to point out that in most economic scenarios there is scope for efficiency-enhancing environmental and agricultural policies. However, since the relevant policy goals are about ecosystem development and sustainability, all serious policies need to focus on the *inter-temporal* development and control of both the ecosystem and the economy. Addressing these issues using the integrated analytical framework suggested here appears to be promising.

As was pointed out in the introduction, the common feature of the approach suggested here and the line of research followed by Tschirhart and others is to explain intra-ecosystem transactions with the help of optimising behaviour of individual organisms. But Tschirhart and others use prices to co-ordinate transactions ('price approach') while we have modelled short-run ecosystem interactions as a non-co-operative game with the Cournot–Nash equilibrium being the pertinent solution concept ('Nash approach').[27] Concerning the price approach, Finnoff and Tschirhart (2002) is the only paper that like the present paper links the analysis of species interactions to endogenous economic activity (fishery). But these authors focus on numerical dynamic analysis while our main attention was placed on the analysis and the comparative statics of short-run ecological equilibrium. Also, Finnoff and Tschirhart (2002) do not study and compare different behavioural attitudes of the fishery toward ecosystem interdependence and the implied normative consequences. To the best of our knowledge, our discussion of ignorant, conventional and green farming is an innovative contribution in the framework of a simple but rigorous model of ecosystem–economy interactions. To study the comparative merits of the

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[27] However, Pethig and Tschirhart (2002) employ neither prices nor Cournot–Nash behaviour but explain resource competition between plants by crowding.

Nash and the price approach, and to compare both of them to procedures put forward in ecological science (the individual-based approach, in particular), is an important topic for future research.

Appendix A. Biomass transactions and energy needed for maintenance

Rather than using Eq. (3) as the basic building block of the model consider;

$$g = (\tilde e_{og}x^{\mathrm{d}}_{og} - \tilde e_g x^{\mathrm{s}}_{gm} - \tilde r_{ga})(1-\alpha_g), \tag{A.1a}$$

$$m = T(m_p, p)(\tilde e_{gm}x^{\mathrm{d}}_{gm} - \tilde e_m x^{\mathrm{s}}_{mb} - \tilde r_{mf} - \tilde r_{ma})(1-\alpha_m), \tag{A.1b}$$

$$b = (\tilde e_{mb}x^{\mathrm{d}}_{mb} - \tilde r_{bf})(1-\alpha_b), \tag{A.1c}$$

where g, m and b are net energy, as in (3) and where the symbols with a tilde ($\sim$) are defined as the corresponding terms without a tilde in (3). α_i denotes the energy used for maintenance (respiration, metabolism etc.) per unit of (gross) energy, $\alpha_i \in][0, 1[$. The superscripts s and d refer to amounts of biomass supplied and demanded, respectively.

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 run. Since biomass intake by a predator must equal the biomass outflow from its prey we require,

$$n_g x^{\mathrm{s}}_{gm} = n_m x^{\mathrm{d}}_{gm} \quad \text{and} \quad n_m x^{\mathrm{s}}_{mb} = n_b x^{\mathrm{d}}_{mb}. \tag{A.2}$$

It is assumed that all predators' demands prevail. Therefore, x^{s}_{gm} and x^{s}_{mb} are substituted in (A.1) by $(n_m/n_g)x^{\mathrm{d}}_{gm}$ and $(n_b/n_m)x^{\mathrm{d}}_{mb}$, respectively. In addition, we suppress all population variables, since populations are constant in the short run, and we further simplify the notation by setting $e_{ij} := \tilde e_{ij}(1-\alpha_j)$, $e_j := \tilde e_j(1-\alpha_j)$, $r_{ia} := \tilde r_{ia}(1-\alpha_i)$ and $r_{if} := \tilde r_{if}(1-\alpha_i)$. Thus, (A.1) and (A.2) are transformed into (3) (with populations being dropped to avoid clutter).

Appendix B. Derivation of (13)

We insert r_{ga} from (8) into (7a): $G^{\mathrm{o}}(\cdot) = e_{og}Y^{og}(\ell_g, m, s) - e_g A^g[R^{ga}(y_{gm})]y_{gm} - R^{ga}(y_{gm})$. Differentiation yields $\mathrm{d}g = e_{og}\underset{+}{Y^{og}_{\ell}}\,\mathrm{d}\ell_g + e_{og}\underset{-}{Y^{og}_{m}}\,\mathrm{d}m + e_{og}\underset{+}{Y^{og}_{s}}\,\mathrm{d}s - [(e_g A^g_r + 1)R^{ga}_y + e_g a_g]\,\mathrm{d}y_{gm}$. Since $e_g A^g_r + 1 = 0$ is the FOC for maximising G^{o} with respect to r_{ga}, we obtain:

$$g = G^1(\underset{+}{\ell_g}, \underset{-}{m}, \underset{+}{s}, \underset{-}{y_{gm}}). \tag{B.1}$$

(B.1) and y_{gm} from (10) readily imply,

$$G\left[\underset{+}{\ell_g}, \underset{-}{m}, \underset{+}{s}, \underbrace{\bar Y^{gm}\underset{+}{(g)}}_{-}\right] = \hat G(\underset{+}{\ell_g}, \underset{-}{m}, \underset{+}{s}). \tag{13a}$$

Consider next r_{mf} and r_{ma} from (8) in (7b):

$$\begin{aligned} M^{\mathrm{o}}(\cdot) = T(m_p, p)\{&e_{mg}a_g Y^{gm}[g, R^{mf}(a_g)] \\ &- e_m A^m[R^{am}(y_{mb})]y_{mb} \\ &- R^{ma}(y_{mb}) - R^{mf}(a_g)\}. \end{aligned}$$

We differentiate this equation totally and take into account that $e_m y_{mb}A^m_r + 1 = 0$ and $e_m a_g Y^{gm}_r = 1$ is implied by maximising M^{o} with respect to r_{mf} and r_{ma}. This calculation yields

$$\begin{aligned} \mathrm{d}m = &\underbrace{m_p T_p}_{-}\,\mathrm{d}p + T(m_p, p)e_{mg}y_{gm}\,\mathrm{d}a_g \\ &+ T(m_p, p)e_{mg}a_g\underset{+}{Y^{gm}_g}\,\mathrm{d}g - \theta_{em}a_m\,\mathrm{d}y_{mb} \end{aligned}$$

and hence

$$m = M^1(\underset{?}{a_g}, \underset{?}{g}, \underset{-}{p}, \underset{-}{y_{mb}}). \tag{B.2}$$

Since $\theta_p > 0$, $T_p = -m_p\delta(m_p)\theta_p < 0$, but the sign of M^1_a and M^1_g depends on the sign of $T(m_p, p)$. Invoking a_g and y_{mb} from (10) transforms (B.2) into $m = M^1[\bar A^g(g), g, p, \bar Y^{mb}(k, m)]$. Differentiation yields:

$$\begin{aligned} \mathrm{d}m = &\frac{M^1_a\bar A^g_g + M^1_g}{1 - M^1_y\bar Y^{mb}_m}\,\mathrm{d}g + \frac{M^1_p}{1 - M^1_y\bar Y^{mb}_m}\,\mathrm{d}p \\ &+ \frac{M^1_y\bar Y^{mb}_k}{1 - M^1_y\bar Y^{mb}_m}\,\mathrm{d}k. \end{aligned} \tag{B.3}$$

The second and third terms on the right side of (B.3) are negative. The numerator of the first term is $M^1_g + M^1_a\bar A^g_g$. Analogous to (11) $M^1_g = T(m_p, p)e_{mg}a_g Y^{gm}_g$

is the direct effect of grain on mice via the impact of grain on mice preying productivity. On the other hand,

$$M_a^1 \bar{A}_g^g = T(m_p, p) e_{mg} y_{gm} \frac{A_r^g R_y^{ga} Y_g^{gm}}{1 - A_r^g R_y^{ga} Y_r^{gm} R_a^{mf}}$$

represents the indirect effect of g on m caused by a growing grain population stepping up its defence. It is plausible to assume that the sign of the net effect is always determined by the sign of the direct effect, M_g^1. Hence,

$$M^1[\bar{A}^g(g), g, p, \bar{Y}^{mb}(k, m)] = \hat{M}(\underset{+}{g}, \underset{-}{k}, \underset{-}{p}), \qquad \text{(13b)}$$

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 insert a_m from (10) and r_{bf} from (8) into (7c):

$$\begin{aligned} B^{\mathrm{o}}(\cdot) = {} & e_{mb} \bar{A}^m(k, m) Y^{mb}\{k, m, R^{bf}[\bar{A}^m(k, m)]\} \\ & - R^{bf}[\bar{A}^m(k, m)]. \end{aligned}$$

Since $e_{mb} a_m Y_r^{mb} = 1$ holds when B^{o} is maximised with respect to r_{bf}, differentiation results in

$$\begin{aligned} \mathrm{d}b = {} & e_{mb}(y_{mb} \underset{-}{\bar{A}_k^m} + a_m \underset{+}{Y_k^{mb}})\, \mathrm{d}k \\ & + e_{mb}(y_{mb} \underset{-}{\bar{A}_m^m} + a_m \underset{+}{Y_m^{mb}})\, \mathrm{d}m. \end{aligned} \qquad \text{(B.4)}$$

For $v = k, m$, the right side of (B4) is symmetric. Y_v^{mb} is the direct and positive effect on buzzard predation productivity while $y_{mb} \bar{A}_v^m < 0$ is the reduction in predation success caused by defensive response of mice to increases in v. It appears plausible, again, to assume that the positive direct effect overcompensates the indirect effect. Hence,

$$B^{\mathrm{o}}\{\bar{A}^m(k, m), k, m, R^{bf}[\bar{A}^m(k, m)]\} = \hat{B}(\underset{+}{k}, \underset{+}{m}). \qquad \text{(13c)}$$

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