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Evolutionary strategies and nutrient cycling in ecosystems

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ABSTRACT

We have previously shown that the presence of a consumer in an ecosystem model at ecologically stable equilibrium (ECSE) results in smaller energy and nutrient flows through the system compared to one without a consumer. Here we extend this analysis to examine energy and nutrient flows, and the density and number of species in ecosystems at evolutionarily stable equilibrium (EVSE). To implement the analysis, we first clarify the difference between ECSE and EVSE, and extend the idea of evolutionarily stable strategies as implemented to biological communities to include the non-animated parts of the ecosystem. In a game theoretic sense, this is equivalent to adding external inputs to the game. EVSE solutions of our model ecosystem resulted in frequently observed trends. For example, of two competing producers, one has smaller density, grows faster, is more nutritious to the consumer, and cycles nutrients faster than the other. In both kinds of ecosystem conditions (ECSE and EVSE), adding producer species to a system with a consumer and producer increases the flow through the ecosystem. We also show that a consumer with a high ratio of return of nutrients to the decomposer compartment compared to the losses to the ecosystem from the consumer compartment cannot co-exist with producers at EVSE. At EVSE, the presence of a consumer increases energy flows compared to systems without a consumer, in contrast to a system at ECSE, where the presence of a consumer decreases rates of energy flow. Finally, we interpret the dynamics of the strategies in the context of periodic input to the ecosystem. We show that strategies can be out of phase, thus enabling, for example, species to exploit a resource more (or less) efficiently at different times.

Keywords: evolutionarily stable strategies, game theory, nutrient cycling.

INTRODUCTION

According to the traditional view of evolutionary games (Maynard-Smith and Price, 1973; Maynard-Smith, 1982; Vincent and Brown, 1988), organisms interact and their strategies (phenotypic or genotypic) co-evolve. Except for perhaps admitting some constraints, the abiotic part of the ecosystem is largely ignored (but see Vincent and Vincent, 1996). Yet, co-evolving organisms do change their environment and thereby affect their own

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co-evolution. Here we develop a formal framework for including the abiotic part of an ecosystem – in which organisms co-evolve – in the evolutionary process. Using this formal framework we examine some commonly held notions about the role of herbivores in cycling nutrients in ecosystems and how these relate to biodiversity. We also pay attention to the issue of stability in the context of evolutionarily stable strategies (ESS), which seem to be of particular interest to evolutionary ecologists (see Eshel and Motro, 1981; Eshel, 1983; Taylor, 1989; Abrams *et al.*, 1993).

Over the past 15 years, there has been increased recognition of interactions between the food web and the cycling of limiting nutrients (Chew, 1974; Mattson and Addy, 1975; Owen and Wiegert, 1976, 1981; Oksanen *et al.*, 1981; Petelle, 1982; Oksanen, 1983, 1988; DeAngelis and Gross, 1992). The conclusion that emerged from this recognition is that herbivores increase the rate of nutrient cycling because the turnover rates of their bodies and faecal material are faster than that of live plants and their shed litter (Chew, 1974; Mattson and Addy, 1975; Owen and Wiegert, 1976, 1981; Petelle, 1982). This has led to a debate about whether plants can increase their fitness by allowing herbivores to eat them (Belsky, 1986, 1987; McNaughton, 1985). Loreau (1995) analysed a simplified ecosystem model (a nutrients pool, producers, consumers and decomposer compartments) and concluded that consumers almost always maximize energy and nutrient flow through ecosystems. Pastor and Cohen (1997) analysed a model similar to that proposed by Loreau (1995). The model includes a nutrients pool, two (or one) producer species, a consumer and a decomposer compartment. The producers differ in related attributes: one of them is more palatable, takes up nutrients from the nutrients pool and releases them to the decomposer compartment at a faster rate, and both producers compete. We then showed that when there is more than one producer in the ecosystem, and the consumer chooses among them, consumers in fact can decrease energy and nutrient flow through ecosystems in stable equilibrium compared to a system where the consumer is absent.

The discussion by both Loreau (1995) and Pastor and Cohen (1997) concentrated on nutrients and energy flow in ecosystems at ecologically stable equilibria (ECSE). Here, we address the following issues: What are the rates of nutrients and energy flows through the ecosystem at evolutionarily (as opposed to ecologically) stable equilibria? What is the role of the consumer in maintaining such flows? How sensitive are the flows and densities of organisms and material in the ecosystem compartments (nutrients, producers, consumers and decomposers) to biologically important parameter ratios.

To address these issues, we need to formally extend the concept of evolutionarily stable strategies in ecological communities to ESS in ecosystems. Vincent and Vincent (1996) addressed these issues in a somewhat different context. The reason for the extension is that, in mathematical models of ecological communities, all participants evolve; in ecosystem models, some components (physical compartments such as nutrients pool) do not evolve, but affect the outcome of the evolutionary 'game'. Yet, the co-evolutionary process affects these abiotic components. From a mathematical game theoretic perspective, such abiotic components (which can be viewed as constraints) may change the 'rules' of the game (e.g. in the prisoner's dilemma game, the negotiating prisoner would rather stay in jail if she knew that there is a lynching mob outside the jail-house).

In a modelling context, a strategy may be viewed as a potentially evolving parameter-value. Examples are the maximum rate of growth of a plant, the efficiency of converting light energy to energy stored in biomass, and the rate at which plant material decays to produce available nitrogen in the soil. In the co-evolutionary process, the strategy-values,

and therefore the density of energy – or some other surrogate measure of energy, such as biomass or nutrient content – of various ecosystem compartments all change because of evolutionary mechanisms. In an idealized ecosystem, these changes may reach a stable equilibrium. The strategy-values at this stable equilibrium are called evolutionarily stable strategies if no other strategy value can co-exist with them. When the strategies reach their evolutionarily stable values, and the ecosystem is at ECSE, the ecosystem is said to have reached its evolutionarily stable equilibrium (EVSE). At such equilibrium, individuals that possess strategy-values other than the ESS (the so-called mutants) cannot co-exist: the ecosystem resists invasion.

ECOSYSTEM STABILITY AND THE EVOLUTIONARY GAME IN AN ECOSYSTEM CONTEXT

The ESS maximum principle

The development in this section is a formal extension of the work of Vincent *et al.* (1996). The extension amounts to formalizing the fact that, in ecosystem models, the governing (differential) equations include variables that represent both abiotic and biotic (usually species densities) quantities. As opposed to the biotic variables, the abiotic variables do not co-evolve. However, because the mass balance of nutrient flows affect the evolutionary process, the abiotic variables affect the co-evolutionary process of the biotic components of the ecosystem, and are in turn affected by the biotic components. We envision a compartment ecosystem model. There are r abiotic resources (e.g. nutrients, water) and s biotic compartments. Each compartment is measured in units of biomass density (e.g. $\mathrm{kg \cdot ha^{-1}}$). Each biotic compartment includes biomass density of a collection of individuals belonging to the same species.

The density of each of the resource compartments is denoted by y_i, and all of them form an r dimensional vector:

$$\mathbf{y} = [y_1, \ldots, y_r]$$

The density of each of the biotic compartments is denoted by x_i, and all of them form an s dimensional vector:

$$\mathbf{x} = [x_1, \ldots, x_s]$$

All of the compartments form an $r + s$ vector:

$$\mathbf{X} = [\mathbf{y}, \mathbf{x}]$$

Each of the biotic compartments (species) has corresponding n strategies; that is, species i's strategy-values are represented by

$$\mathbf{u}_i = [u_i^1, \ldots, u_i^n]$$

and the set of all strategies is represented by a matrix

$$\hat{\mathbf{u}} = [\mathbf{u}_1, \ldots, \mathbf{u}_s]$$

We assume that the strategies belong to some strategy space, U. A species is represented by a collection of individuals. These individuals can interbreed, they all use the same strategies and they all may have distinct values for their strategies (there is phenotypic variance). $\mathbf{u}_i$ represents their mean value and they occupy a single ecosystem compartment.

The ecosystem is modelled by a set of $r + s$ coupled ordinary differential equations:

$$\left.\begin{aligned} \dot{y}_i &= f_i(\hat{\mathbf{u}}, \mathbf{X}(t)) \qquad i = 1, \ldots, r \\ \dot{x}_i &= x_i(t) H_i(\hat{\mathbf{u}}, \mathbf{X}(t)) \quad i = 1, \ldots, s \end{aligned}\right\} \tag{1}$$

where dots denote derivatives with respect to time and H_i represents the individual instantaneous fitness function for individuals of species i. The functions f_i and H_i are presumed to have continuous partial derivatives with respect to $\mathbf{X}$ and $\hat{\mathbf{u}}$.

Because we wish to deal with existing species (densities are greater than zero), the non-negative orthant is defined by

$$\Re = \{\mathbf{X} \in R^{r+s} | \mathbf{X} \geq 0\}$$

where R^{r+s} is an $r + s$ dimensional real state space. For model (1) to make sense, we require that:

- $y_i(t) > 0$ for all t and for $i = 1, \ldots, r$;
- $x_i(t) > 0$ for all t and for $i = 1, \ldots, \rho$ $(1 \leq \rho \leq s)$;
- $x_i(t) = 0$ for all t and for $i = \rho + 1, \ldots, s$;
- $\mathbf{X}$ occupies a subset of $\Re$.

Given $\hat{\mathbf{u}}$, a point $\mathbf{X}^* = [\mathbf{y}^*, \mathbf{x}^*] \in \Re$ is said to be an ecosystem equilibrium point of equation (1) provided that there exists a ρ such that

$$\begin{aligned} &1 \leq \rho \leq s \\ &f_i(\hat{\mathbf{u}}, \mathbf{X}^*) = 0 \qquad \text{for } i = 1, \ldots, r \\ &H_i(\hat{\mathbf{u}}, \mathbf{X}^*) = 0 \qquad \text{for } i = 1, \ldots, \rho \\ &x_i^* = 0 \qquad\qquad\ \ \text{for } i = \rho + 1, \ldots, s \end{aligned} \tag{2}$$

When $r = 0$ in equation (2), the definition of ecosystem equilibrium point becomes identical to the definition of ecological equilibrium point (given in Vincent *et al.*, 1996). Next, we define a ball, B, centred at $\mathbf{X}^*$, as the set of points in the $r + s$ dimensional space with a Euclidean norm E^{r+s} satisfying

$$B = \{\mathbf{X} \in E^{r+s} \| \mathbf{X} - \mathbf{X}^* \| < \varepsilon\} \tag{3}$$

Given $\hat{\mathbf{u}} \in U$, the point $\mathbf{X}^* \in \Re$ is said to be an ecosystem stable equilibrium point if there exists a B such that, for any $\mathbf{X}(0) \in \Re \cap B$, the solution of equation (1) satisfies $\mathbf{X}(t) \in \Re$ for all t, and

$$\lim_{t \to \infty} \mathbf{X}(t) = \mathbf{X}^* \tag{4}$$

A local (global) stable ecosystem equilibrium point is referred to as a local (global) ecosystem stable equilibrium (ECSE). We will not pursue global stability further (see Vincent *et al.*, 1996) and, unless otherwise stated, when we talk about stability, we mean local stability. Note that, with $r = 0$, the definition of ECSE corresponds to the definition of ecological stable equilibrium given in Vincent *et al.* (1996).

Next, we define the following matrices:

$$\mathbf{D}_{11} = \begin{bmatrix} \frac{\partial f_1}{\partial y_1} & \cdots & \frac{\partial f_1}{\partial y_r} \\ \vdots & \ddots & \vdots \\ \frac{\partial f_r}{\partial y_1} & \cdots & \frac{\partial f_r}{\partial y_r} \end{bmatrix}, \mathbf{D}_{12} = \begin{bmatrix} \frac{\partial f_1}{\partial x_1} & \cdots & \frac{\partial f_1}{\partial x_\rho} \\ \vdots & \ddots & \vdots \\ \frac{\partial f_r}{\partial y_1} & \cdots & \frac{\partial f_r}{\partial x_\rho} \end{bmatrix}, \mathbf{D}_{13} = \begin{bmatrix} \frac{\partial f_1}{\partial x_{\rho+1}} & \cdots & \frac{\partial f_1}{\partial x_s} \\ \vdots & \ddots & \vdots \\ \frac{\partial f_r}{\partial x_{\rho+1}} & \cdots & \frac{\partial f_r}{\partial x_s} \end{bmatrix},$$

$$\mathbf{D}_{21} = \begin{bmatrix} x_1\frac{\partial H_1}{\partial y_1} & \cdots & x_1\frac{\partial H_1}{\partial y_r} \\ \vdots & \ddots & \vdots \\ x_\rho\frac{\partial H_\rho}{\partial y_1} & \cdots & x_\rho\frac{\partial H_\rho}{\partial y_r} \end{bmatrix}, \mathbf{D}_{22} = \begin{bmatrix} x_1\frac{\partial H_1}{\partial x_1} & \cdots & x_1\frac{\partial H_1}{\partial x_\sigma} \\ \vdots & \ddots & \vdots \\ x_\rho\frac{\partial H_\rho}{\partial x_1} & \cdots & x_\rho\frac{\partial H_\rho}{\partial x_\rho} \end{bmatrix},$$

$$\mathbf{D}_{23} = \begin{bmatrix} x_1\frac{\partial H_1}{\partial x_{\rho+1}} & \cdots & x_1\frac{\partial H_1}{\partial x_s} \\ \vdots & \ddots & \vdots \\ x_\rho\frac{\partial H_\rho}{\partial x_{\rho+1}} & \cdots & x_\rho\frac{\partial H_\rho}{\partial x_s} \end{bmatrix}$$

With these definitions, we get that given $\hat{\mathbf{u}} \in U$, if an ecosystem equilibrium point $\mathbf{X}^*$ is an ECSE, then all the eigenvalues of the matrices

$$\mathbf{D} = \begin{bmatrix} \mathbf{D}_{11} & \mathbf{D}_{12} \\ \mathbf{D}_{21} & \mathbf{D}_{22} \end{bmatrix}_{(\hat{\mathbf{u}}, \mathbf{X}^*)} \tag{5}$$

$$\mathbf{H} = \begin{bmatrix} H_{\rho+1} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & H_s \end{bmatrix}_{(\hat{\mathbf{u}}, \mathbf{X}^*)} \tag{6}$$

must have negative real parts. Note that we require negative real parts because we are dealing with local stability.

Because $\mathbf{H}$ is diagonal, with real elements, its eigenvalues are the values of the diagonal elements, and in ECSE the fitness of all species with $x_i = 0$ are negative. Next we use the concept of the *G*-function, first introduced by Vincent and Brown (1988). Here we extend the definition to ecosystem.

A function $G(\mathbf{u}, \hat{\mathbf{u}}, \mathbf{X})$ is said to be a fitness generating function for all species in an ecosystem sharing the same strategy set U if

$$G(\mathbf{u}_i, \hat{\mathbf{u}}, \mathbf{X}) = H_i(\hat{\mathbf{u}}, \mathbf{X}) \tag{7}$$

The difference between the *G*-function used here and the one used in Vincent *et al.* (1996) is that we use $\mathbf{X}$ (the vector of both resource and species compartments) instead of $\mathbf{x}$

(the vector of the species alone). To keep the notation simple we use a single *G*-function. This means that all individuals of all species are evolutionarily identical (Brown and Vincent, 1987); that is, changes in strategy values have similar consequences for all individuals. For example, individual plants of two species grow faster if the efficiency of their photosynthesis increases.

Based on the definition of the *G*-function, we may write equation (1) as:

$$\left.\begin{aligned} \dot{y}_i &= f_i(\hat{\mathbf{u}}, \mathbf{X}(t)) \qquad i = 1, \ldots, r \\ \dot{x}_i &= x_i(t) G(\mathbf{u}_i, \hat{\mathbf{u}}, \mathbf{X}(t)) \qquad i = 1, \ldots, s \end{aligned}\right\} \tag{8}$$

The discussion above implies that the density of some species is zero, while that of others is greater than zero. Next, we rearrange the vector $\hat{\mathbf{u}}$ such that for $i = 1, \ldots, \rho$ we have $x_i^* > 0$ and for $i = \rho + 1, \ldots, s$ we have $x_i^* = 0$ (asterisks indicate values at equilibrium). The first set of strategies form the so-called coalition vector and is denoted by

$$\mathbf{u}_c = [\mathbf{u}_1, \ldots, \mathbf{u}_\rho]$$

The coalition vector is an evolutionarily stable strategy for the equilibrium point $\mathbf{X}^*$ if the equilibrium point $\mathbf{X}^*$ is an ECSE. When a system is at ECSE and the strategies are at their ESS values, the ecosystem is said to be at its evolutionarily stable equilibrium (EVSE).

The ESS maximum principle (Vincent *et al.*, 1996) then states that, for the fitness generating function of a community of *s* species, $G(\mathbf{u}, \hat{\mathbf{u}}, \mathbf{X})$, if $\mathbf{u}_c$ is an ESS, then $G(\mathbf{u}, \hat{\mathbf{u}}, \mathbf{X})$ must take on a maximum with respect to $\mathbf{u}$, at $\mathbf{u}_c$. This principle remains valid for the ecosystem (a formal proof of this statement is available from us). Thus, for the definition

$$G^*(\mathbf{u}) \equiv G(\mathbf{u}, \hat{\mathbf{u}}, \mathbf{X}^*) \tag{9}$$

and for unbounded scalar strategies, the ESS maximum principle requires that

$$\left[\frac{\partial G^*}{\partial u}\right]_{u=u_i} = 0,\ G^*(u_i) = 0,\ \left[\frac{\partial^2 G^*}{\partial u^2}\right]_{u=u_i} < 0 \quad \text{for } i = 1, \ldots, \rho \tag{10}$$

Equation (10) is used below in computations of ESS. Note that the maximum principle provides necessary conditions for ESS.

Strategy dynamics

Vincent *et al.* (1993) showed that, for u_i representing the mean value of a strategy for species *i*, and for small and symmetric variance around this mean, strategy dynamics are thus:

$$\dot{u}_i = h\sigma^2 \left.\frac{\partial G(u, \mathbf{u}, \mathbf{x})}{\partial u}\right|_{u=u_i}$$

where *h* is the hereditability coefficient and σ^2 is the genetic variance. This condition remains true for ecosystems. That is,

$$\dot{u}_i = h\sigma^2 \left.\frac{\partial G(u, \mathbf{u}, \mathbf{X})}{\partial u}\right|_{u=u_i} \tag{11}$$

Because the dynamics of the strategy evolve in a game milieu, the question of stability of **u*** at ESS may be subtle. Thus, a few stability conditions were advanced: the convergent stable strategies (Eshel and Motro, 1981; Eshel, 1983), the m and δ stability (Taylor, 1989), and so on. Abrams *et al.* (1993) have also discussed this issue and pointed out that finding an ESS is not enough; one must also check the stability of the strategy dynamics.

It turns out that the necessary conditions of the maximum principle, in particular the requirement of stability on **X***, is also necessary for stability of the strategy dynamics (given the definition of the mean population fitness above). The upshot is that, in analysing an ESS model, you first find a candidate solution to the ESS using the necessary conditions as outlined in the maximum principle. To verify that the candidate is indeed an ESS solution, verify that it indeed gives a local maximum on G and then check for the stability of **X***. A much more detailed analysis of the stability of ESS is given in Cohen *et al.* (1999).

THE ECOSYSTEM MODEL WITHOUT EVOLUTION

Loreau (1995) proposed a simplified ecosystem model which we use as a starting point. His model included the following compartments: a nutrients pool (N), a producer (x), a consumer (C) and two decomposers (D). In the model used by Pastor and Cohen (1997), we removed one of the decomposer compartments and added one more producer compartment. Here, we present a generalization of our previous model. The generalization amounts to including an unspecified number of producer compartments. The number of producer compartments whose densities are positive at the EVSE is treated as a parameter denoted by ρ (see equation 2), and its value is to be determined for the ecosystem at its EVSE. Recall from the definition of the coalition vector that ρ is the number of producer species whose density at the EVSE is positive.

As in Loreau (1995), Pastor and Cohen (1997) modelled the ecosystem as a collection of interacting compartments. Each compartment represents a collection of functionally related species biomass (or its energy equivalent) density (e.g. $kg \cdot ha^{-1}$). In the case of producers, each compartment represents a species. The ecosystem is presumed to be nutrient-limited, and the identified compartments (Fig. 1) are: a nutrient pool (N), s producers ($x_1, \ldots, x_s$), a consumer (C) and a decomposer (D). We assume that the biomass in a compartment is proportional to its nutrient density. Flows to the decomposer are linear donor-controlled, and flows from N to x_i are some functions, $f_i(\cdot)$. The flows from x_i to C are modelled by the functions $g_i(\cdot)$. The system is open, with a constant input rate, Q, and output regulated through linear functions with proportionality parameters, e_i. To reduce the clutter in Fig. 1, the interactions among the producer compartments are not shown.

To make the model identical to that of Loreau (1995), (i) keep only one producer compartment, (ii) add a decomposer compartment and (iii) make all e_i equal. The addition of producer compartments (Fig. 1) reflects the fact that we wish to leave ρ as a parameter ($1 \le \rho \le s$). The elimination of one decomposer compartment reflects the fact that both producers and consumers are decomposed by a single pool, which eventually returns nutrients to the N compartment. To fix ideas, Loreau (1995) used the Lotka-Volterra form for the functions f and g in Fig. 1 and Pastor and Cohen (1997) added

competition among the producers. With these in mind, the ecosystem model in Fig. 1 is written as:

$$\left.\begin{aligned}
\dot{N} &= Q + d_D D - N\left(e_N + \sum_{i=1}^{s} a_i x_i\right) \\
\dot{x}_i &= x_i\left(a_i N - b_i - c_i C - e_i - \sum_{j=1}^{s} m_{ij} x_j\right), \quad i = 1, \ldots, s \\
\dot{C} &= C\left(\sum_{i=1}^{s} c_i x_i - b_C - e_C\right) \\
\dot{D} &= \sum_{i=1}^{s} c_i x_i + b_C C - D(d_D + e_D)
\end{aligned}\right\} \tag{12}$$

The parameters m_{ij} reflect the strength of the competitive effect of x_j on x_i. To simplify the analysis, both Loreau (1995) and Pastor and Cohen (1997) assumed that $e_N = e_1 = \ldots = e_s = e_C = e_D = e$ (see Loreau, 1995, for justification of this assumption).

Pastor and Cohen (1997) compared the nutrients (or equivalent energy) flow through the ecosystem at ECSE both with and without a consumer. As an index of energy flow they used the material flow from N to the consumers. That is,

$$F^* = N^* \sum_{i=1}^{s} a_i^* x_i^* \tag{13}$$

where asterisks indicate quantities at ECSE.

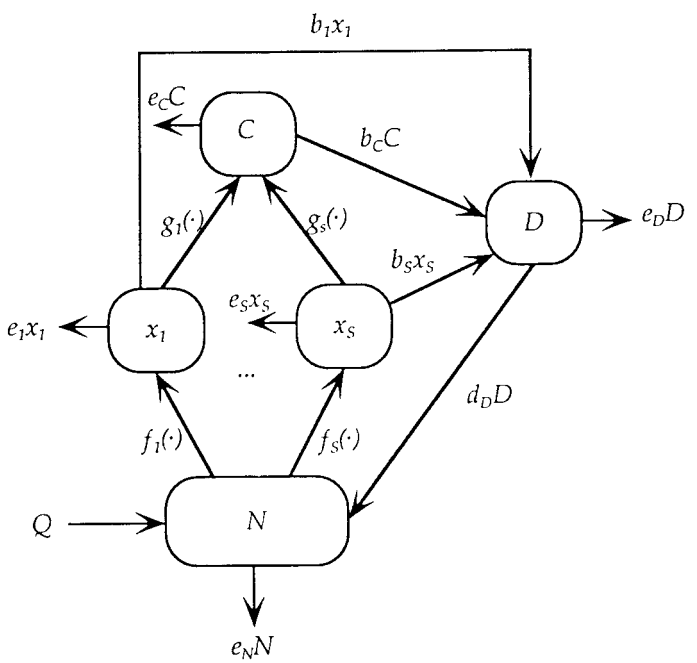

Fig. 1. Model flow diagram (equation 12). Dots in the functions f and g denote as yet unspecified variables and parameters.

Using this example, with $\rho = s = 2$ (and with nutrient uptake rates for each producer correlated with their decay rates and the consumer preference of them), Pastor and Cohen (1997) showed that, for ecosystems at ECSE, a consumer decreases the rate of energy or nutrient flow through the ecosystem, rather than increase it. This conclusion is contrary to conventional wisdom. The fundamental reason for this difference stems from the fact that we used more than one producer species in the ecosystem model and traits influencing nutrient flows are correlated as just stated. This happens even without implementing competition between the producers. With the latter implemented, our results were further accentuated.

THE ECOSYSTEM MODEL WITH EVOLUTION

Traditional analyses of model ecosystems examine the stability of ECSE. Species in ecosystems co-evolve, and the co-evolutionary process, with the presumed maximization of fitness of participating organisms, may lead to an increase in the cycling of energy or nutrients within the ecosystem. Such a possibility calls for evaluation of the model (equation 12) in the context of ESS. The question we wish to address is: Can we expect the presence of a consumer to increase energy flow through the ecosystem at its EVSE? Furthermore, we wish to allow co-evolution to dictate how many producer species co-exist; in other words, ρ in equation (10) becomes a parameter whose value is to be determined by the ecosystem model at EVSE, rather than fixed at 1 (Loreau, 1995) or 2 (Pastor and Cohen, 1997). We also wish to investigate the range of interesting parameter values for which candidate EVSE solutions exist, and the density of compartments at these solutions.

Here, EVSE means the following. Each producer species has a number of heritable traits (strategies) whose specific values determine the fitness of individuals. For example, a limited supply of nitrogen affects the growth rate of different (individuals of a) plant species by a different amount. In this example, one may construct a model with a parameter, u, whose value sums up the variety of mechanisms in plants that function in the uptake of nitrogen. Different plant species will then have different values for the parameter u at the EVSE. The parameter u represents an evolutionary strategy, and species are defined as a collection of individuals having an identical mean value for the strategy.

At the EVSE we have an assembly of specific values of u ('species'), with the corresponding population densities positive (the coalition). Individuals with different strategy values from those of the coalition are called mutants. In an ecosystem at EVSE, mutants eventually become extinct. By extinction we mean that either the density of mutants goes to zero, or the value of their strategy evolves to that of one of the coalition species. Our task, then, is to determine the values of the strategy u at EVSE, and how much such unique values (species) co-exist.

Next, we incorporate these ideas in the ecosystem model (equation 12). But first, for better or worse, a few simplifying assumptions:

1. The ecosystem includes a single consumer that is not co-evolving. This happens (approximately) in ecosystems where either lack of genetic variation or gene flow from elsewhere could prevent the consumer from evolving in response to changes in producers. The main reason for using this simplifying assumption is that the addition of

a co-evolving consumer would require an additional fitness generating function. This complicates the model, and we argue that it is important to first thoroughly understand the simpler model before moving on to more complex and perhaps more realistic models of co-evolution.

2. Producers evolve due to direct intra- and inter-specific competition among themselves and due to indirect competition via uptake of nutrients and consumption by the consumer.
3. Rates such as nutrient uptake, consumption and nutrient losses are all correlated (Coley *et al.*, 1985; Bryant and Chapin, 1986; Pastor and Cohen, 1997). For example, it is well known that plant species that have higher tannins and lignin concentrations in their tissue (compared to other species) are less preferred by herbivores (consumption rate lower), their decay rate is slower, their tolerance to conditions such as low light and low nitrogen is higher, and their growth rate is slower (Bryant and Kuropat, 1980; Bryant and Chapin, 1986; Bryant *et al.*, 1991). Numerous examples of the correlations between plant tissue chemistry, nutrient uptake rates, herbivore preference and decomposition rate have been reviewed elsewhere (Bryant and Kuropat, 1980; Coley *et al.*, 1985; Bryant and Chapin, 1986; Horner *et al.*, 1988; Bryant *et al.*, 1991; Huntly, 1991; Pastor and Naiman, 1992). In other words, some of the relevant ecosystem attributes of such plants are correlated through an important evolutionary strategy: the concentration of defensive compounds in plant tissue. Thus, one may use a single evolutionary strategy, u, which summarizes these correlations. A single strategy-value results in different values for these rates. As in the case of assumption (1), the addition of a vector of strategies will complicate the model and distract from our main points. It is also important to understand thoroughly the case with a single strategy before moving on to multiple strategies.
4. For obvious reasons, the nutrient compartment, N (Fig. 1), does not co-evolve, although the flows through it are affected by the densities of species and their strategy values (equation 8).
5. Because it is donor controlled, the decomposer compartment D (Fig. 1) does not co-evolve.
6. The EVSE determines the number of producer species only, there is no distinction among the consumer species (a single functional 'species'), and there is no distinction among the decomposer species.

We recast the ecosystem model (equation 12) in an evolutionary framework (similar to equation 8) and then discuss its interpretation. The parameters a_i, b_i, c_i, e_i and m_{ij} in equation (12) become functions of the single evolutionary strategy u:

$$\left.\begin{aligned} a(u) &= k_a \exp\left(\frac{-u^2}{\sigma_a}\right), \quad b(u) = k_b \exp\left(\frac{-u^2}{\sigma_b}\right), \quad c(u) = k_c \exp\left(\frac{-u^2}{\sigma_c}\right), \\ e(u) &= k_e \exp\left(\frac{-u^2}{\sigma_e}\right), \quad m(u, u_i) = k_1 + \exp\left(-\frac{(u - u_i + k_2)^2}{\sigma_m}\right) \end{aligned}\right\} \tag{14}$$

Equation (12) now becomes:

$$\left.\begin{aligned}
\dot{N} &= Q + d_D D - N\left(e_N + \sum_{i=1}^{\sigma} a(u_i)x_i\right) \\
\dot{x}_i &= x_i\left[a(u_i)N - b(u_i) - c(u_i)C - e(u_i) - \sum_{j=1}^{\sigma} m(u_i, u_j)x_j\right], \quad i = 1, \ldots, \sigma \\
\dot{C} &= C\left[\sum_{i=1}^{\sigma} c(u_i)x_i - b_C - e_C\right] \\
\dot{D} &= \sum_{i=1}^{\sigma} c(u_i)x_i + b_C C - D(d_D - e_D)
\end{aligned}\right\} \tag{15}$$

The state variables that are denoted by capital letters in equation (15) correspond to y_i in equation (8). Note that, in equation (15), we use $\rho = s$. The generic functions a, b, c and e in equation (14) use scalers, k, and the subscripted parameters σ. The exponential forms in equation (14) were chosen because of their mathematical convenience and because we wish to avoid dealing with EVSE at the boundaries of u. Thus, there is a particular value of the strategy that maximizes (or minimizes) the rate functions in equation (14). This exponential form is useful because strategy values operate within biological and physical constraints, and thus have some optimal values. The exponential forms in equation (14) also allow negative values for the strategies. The subscripted parameters σ provide some measure of 'stiffness': smaller values mean that deviations of the strategy from its (yet to be determined) ESS value(s) results in a large reduction (or increase) in the fitness at the EVSE (compared to larger values of subscripted σ). Thus, σ behaves like the variance in the normal distribution.

The competition function $m(u, u_i)$ in equation (14) may be interpreted as follows: k_1 and k_2 are scalers. The parameter σ_m scales the amount of reduction in the strength of competition when u deviates from its yet to be determined ESS value u_i*. Larger σ_m means a smaller reduction in the strength of (intra- or inter-specific) competition when u deviates from u_i*. This particular form of modelling competition has been traditionally used by Vincent and co-workers and others cited therein to model competition in co-evolving Lotka-Volterra population models (see Vincent and Brown, 1988; Cohen and Vincent, 1997). We return to this point below.

One of the assumptions implied in equation (14) is that the evolutionary trait that maximizes the consumption of nutrients by the producer, $a(u)$, also maximizes their decay rate, $b(u)$, their consumption rate by the consumer, $c(u)$, and their loss rate, $e(u)$. These typical trends co-occur; for example, compare deciduous to conifer plant species in mixed hardwood forests in North America. In northern mixed forests, deciduous species such as birch (*Betula papyrifera*) and aspen (*Populus tremuloides*) have faster growth rates, nutrient uptake rates, higher nutrient concentrations, faster decay rates, and are more preferred by consumers than slow growing conifers such as spruce (*Picea glauca*, *P. mariana*), fir (*Abies balsamea*) or pines (*Pinus strobus*, *P. resinosa*, *P. banksiana*) (Van-Cleve and Oliver, 1982; Flanagan and Cleve, 1983; Moore, 1984; Coley *et al.*, 1985; Bryant and Chapin, 1986).

The ecosystem model (equation 15) assumes that there are ρ producer species x_i whose densities are positive (ρ is a parameter whose value is to be determined by the solution procedure as given in equation 10), one consumer species (C), the nutrient pool (N) and the decomposer compartment (D). The producers compete according to the function m.

Each producer species has a yet to be determined strategy value u_i. Thus, according to the notation in equation (1), $\mathbf{y} = [N, C, D]$.

The right-hand side of the producer equations in (15) embody the classical Lotka-Volterra competition model where individuals of all producer species compete among and within themselves. This is expressed through the summation term. When u replaces u_i in each of the x_i equations, the term in the square brackets for the producer equations (the producer fitness function) represents the *G*-function of the producers. Thus,

$$G(u, \hat{\mathbf{u}}, \mathbf{X}) = a(u)N - b(u) - c(u)C - e(u) - \sum_{i=1}^{\sigma} m(u, u_i)x_i \tag{16}$$

As in equation (13), the energy flow through the ecosystem at EVSE is calculated according to:

$$F^* = N^* \sum_{i=1}^{\sigma^*} a(u_i^*)\, x_i^* \tag{17}$$

Asterisks in equation (17) indicate quantities at EVSE.

THE CHOICE OF PARAMETERS FOR SENSITIVITY ANALYSIS OF ESS CANDIDATE SOLUTIONS

Here, we are interested in exploring the range of some parameter values, for which EVSE candidate solutions exist for ecosystems with one or two producer species, and with or without a consumer species. By EVSE solutions we mean those solutions that: (i) give positive values for the state variables (N, x_i, D and C where appropriate), as required by equation (2); (ii) fulfil the requirements of equation (10); and (iii) result in negative real parts of the eigenvalues of the matrix **D** (equation 5). We chose combinations of parameter values, and calculated EVSE candidate solutions for those. Unless otherwise stated, all of the results below satisfy the three conditions above.

It should be emphasized that because the ESS maximum principle gives necessary conditions, there is no guarantee that the solutions we found are EVSE; that is why we call them candidate EVSE solutions. To verify that the candidates are indeed EVSE, we ran simulations on the dynamics of the system with a selected set of parameter values (equations 14 and 15). The simulations included producer species (one or two) with their ESS values and additional (non-coalition) species with strategy values other than those of the ESS. In all of the simulations, all of the non-ESS species eventually became extinct. This amounts to verifying that the correct value of ρ (equations 5 and 6) was chosen for the solution. We shall talk about dynamics later. The simulations results then indicate that the candidate EVSE we found are most likely EVSE. Strictly speaking, however, we are dealing with candidate EVSE.

Recall (from Fig. 1 and equation 15) that d_D is a parameter that reflects the proportion (of D) of the nutrients (or their energy equivalent) in the decomposer compartment that is returned to the nutrients compartment. Furthermore, e_D is the proportion of the nutrients in the decomposer compartment that is lost from the ecosystem. The ratio d_D/e_D may be viewed, from the ecosystem 'perspective', as the efficiency of nutrient cycling by the decomposer compartment: The higher the ratio, the larger the proportion of nutrients and energy that are cycled through the decomposer compartment and retained in the system,

compared to those that are lost from the ecosystem by gaseous losses such as denetrification or leaching of soluble organics.

The parameter b_C reflects the proportion (of C) of nutrients that is returned from the consumer to the decomposer, and e_C is the proportion (of C) of nutrients that is lost from the ecosystem through the consumer compartment by migration, for example. Both of these processes (loss and recycling) are modelled as donor controlled. In other words, the ratio b_C/e_C may be viewed, from the ecosystem 'perspective', as some measure of consumer efficiency in cycling nutrients. Similar reasoning applies to the nutrients compartment 'efficiency' in cycling nutrients, Q/e_N. Here e_N corresponds to nutrient losses through processes such as leaching of inorganic forms and volatilization. Thus, we chose to examine the range of values of those parameter ratios (efficiencies) that give candidate EVSE solutions.

The values of the remaining parameters in equations (14) and (15) were kept constant. The constant parameters may be viewed as constraints on the evolution of the system.

THE ECOSYSTEM WITH ONE PRODUCER AND NO CONSUMER AT CANDIDATE EVSE

We established the existence of EVSE candidate solutions for the following values of the model ecosystem parameters (equations 14 and 15 with the consumer equation removed and $\rho = 1$):

$$k_a = 2;\ \sigma_a = 50;\ k_b = 1;\ \sigma_b = 50;\ k_e = 0.1;\ \sigma_e = 50$$
$$k_1 = 2.5;\ k_2 = 2;\ \sigma_m = 50 \qquad (18)$$
$$Q = 50;\ e_N \in (0, 50);\ e_D = 1;\ d_D \in (0, \infty)$$

Outside the parameter ranges, no candidate EVSE solutions exist. Note that because $e_N \in (0, 50)$, we chose to display on one of the axes the inverse nutrient compartment efficiency (e_N/Q) as opposed to its efficiency (Q/e_N) in Fig. 2. The small tilt of the surfaces in the d_D/e_D direction indicates that values of candidate EVSE solutions for N, x and F (Figs 2A, B and D) are not particularly sensitive to the efficiency with which the decomposer compartment cycles nutrients in the ecosystem. For this reason, we display d_D/e_D for the range (0, 5) only. The density D at EVSE becomes more sensitive to changes in decomposer efficiency (d_D/e_D) as the N compartment becomes more efficient (as e_N/Q decreases; Fig. 2C). Thus, in ecosystems at EVSE, low nutrient cycling by decomposers and high nutrient cycling efficiency through nutrient pools should correspond to high densities of decomposers. Similar trends, but less sensitive to changes in parameter values trends, should be exhibited by the nutrient pools, producers and flows.

To verify that all the solutions that form the surfaces shown in Figs 2A–D are indeed EVSE candidates, we examined the G-functions (Fig. 3). Only every tenth G-function that corresponds to the combinations of the ratios d_D/e_D versus e_N/Q are shown. Note that all of the G-functions have a single peak, at $G(u^*) = 0$. This establishes that the solutions shown in Fig. 2 are candidate EVSE.

As the efficiency of D increases and that of N decreases (moving from front to back in Fig. 3), the shape of the G-function becomes flatter around the ESS value (i.e. around the maximum value of G). Each G-function in Fig. 3 represents an adaptive landscape for the

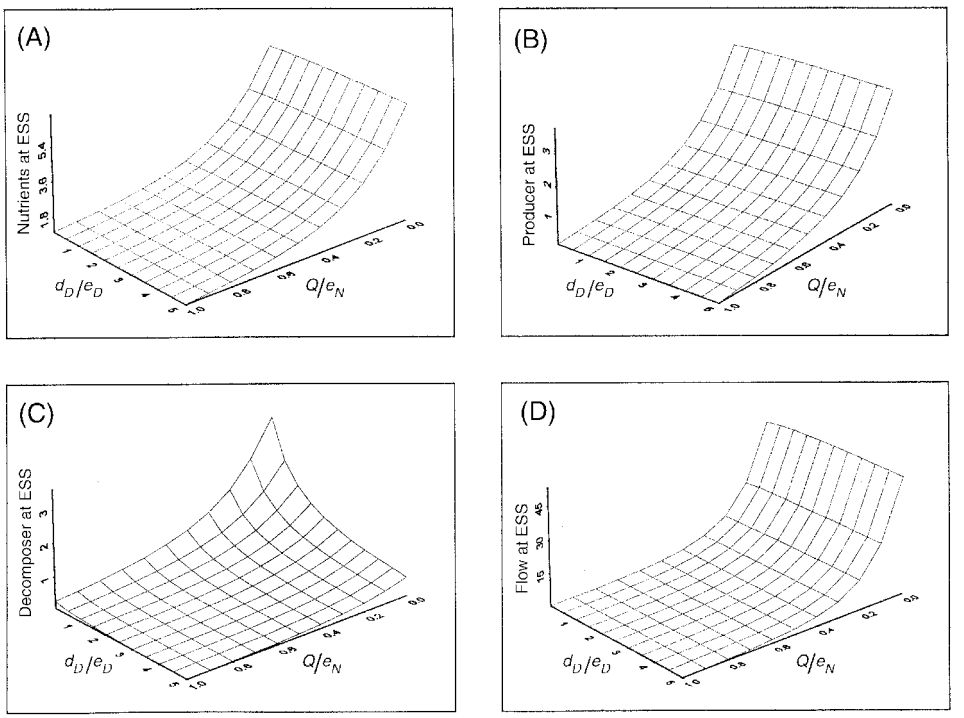

Fig. 2. EVSE candidate solutions for the ecosystem with one producer and no consumer (modified equation 15), and with parameter values and ranges given in equation (18).

combination of the parameter ratios used to generate it. The amount of reduction in the value of the *G*-function for a fixed deviation from either side of the ESS value of the strategy u becomes smaller in systems with more efficient D and less efficient N. This amount of reduction in the value of G can be interpreted as the 'penalty' in fitness that individuals of a species 'pay' when their strategy values deviate from the ESS value. When non-ESS values are played against ESS values in simulations as described above, it takes longer for the producer species with non-ESS values to go extinct in flatter adaptive landscapes. In other words, in ecosystems (as modelled here) with decomposers that are highly efficient in cycling nutrients, and with high rates of nutrient losses through the nutrient compartment (e.g. leaching), one would expect to find more species of producers. This is a surprising result. However, little is known about the efficiency by which decomposers cycle nutrients, rates of leaching loss and their relationship to plant species diversity. Thus, predictions could be considered a test of the model proposed here.

THE ECOSYSTEM WITH ONE PRODUCER AND ONE CONSUMER AT CANDIDATE ESS SOLUTIONS

For the ecosystems with one producer and one consumer (equation 14 and $\rho = 1$ in equation 15), we chose the same values for the fixed parameters as in equation (18). Candidate EVSE solutions were found for the following parameter values and ranges:

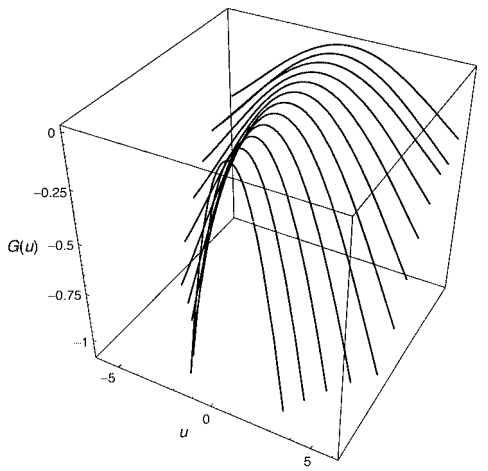

Fig. 3. A stack of $G(u)$ for the system with one producer and no consumer, and the parameter values given in equation (18). Each graph is drawn for a point on the mesh d_D/e_D versus Q/e_N shown in Fig. 2. The graphs are drawn from front to back for increasing values of both d_D/e_D and Q/e_N. Note that (i) in all cases the maximum value of G is at zero, indicating that the solutions drawn in Fig. 2 are EVSE candidates, and (ii) the graphs become steeper as the parameter ratios decrease.

$$\begin{gathered} k_a = 2;\ \sigma_a = 50;\ k_b = 1;\ \sigma_b = 50;\ k_c = 5;\ \sigma_c = 50;\ k_e = 0.1;\ \sigma_e = 50 \\ k_1 = 2.5;\ k_2 = 2;\ \sigma_m = 50;\ Q = 50;\ e_N = 1 \\ e_C = 1;\ b_C \in (0,\ 17);\ e_D = 1;\ d_D \in (0,\ \infty) \end{gathered} \tag{19}$$

(Fig. 4). Candidacy was established by examining the G-functions (Fig. 5) and verifying that they achieve their maxima at zero, checking that the real parts of the eigenvalues of **D** in equation (5) were all negative, and running simulations of equation (15) of species with non-ESS values against those with ESS values and verifying eventual extinctions of the former (i.e. extinction of the non-coalition species).

As in the case of a system with one producer and no consumer, the small tilt of the surfaces (Figs 4A, B and D) in the d_D/e_D direction indicates that the existence of (and density of compartments at) candidate EVSE solutions is only slightly sensitive to the efficiency of D in cycling nutrients in the ecosystem. Unlike the nutrients, producer and consumer compartments, the decomposer's density is sensitive to its efficiency at low values (up to about $d_D/e_D = 5$). We therefore present the surfaces for $0 < d_D/e_D < 5$ only. Outside the range $0 < b_C/e_C < 17$, the solutions became unstable or in some cases the density of one of the compartments became negative. Thus, the results in Fig. 4 represent the parameter space for which candidate EVSE solutions exist.

The existence of EVSE candidate solutions and compartments density at EVSE are sensitive to the efficiency of the consumer in cycling nutrients (Figs 4A–D). The fact that candidate ESS solutions can be found for the range $0 < b_C/e_C < 17$ only indicates that the currency (energy or nutrients) that is returned to D (from C) cannot be too large compared to that lost from the ecosystem (from C). An ever increasingly efficient consumer (Fig. 4C) eventually cannot co-exist at EVSE; it does correspond with a higher density of the pro-

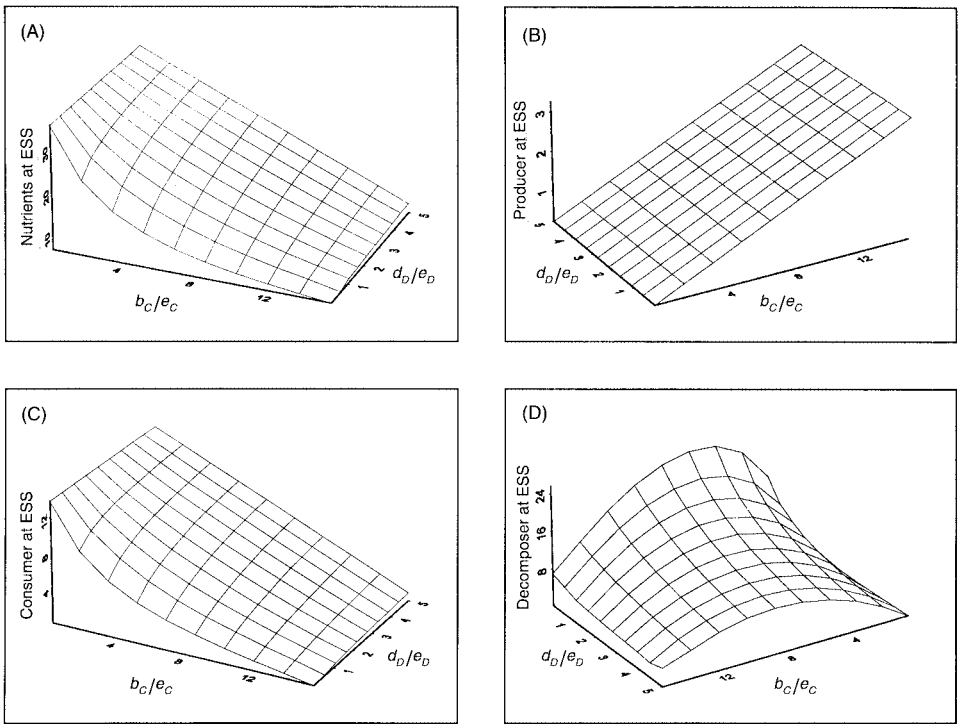

Fig. 4. EVSE candidate solutions for the ecosystem with one producer and one consumer (equation 15), and with parameter values and ranges given in equation (19).

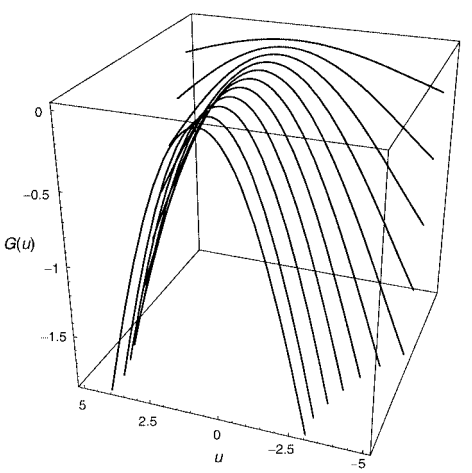

Fig. 5. A stack of $G(u)$ for the system with one producer and one consumer, and the parameter values given in equation (19). Each graph is drawn for a point on the mesh d_D/e_D versus b_C/e_C shown in Fig. 4. The graphs are drawn from back to front for increasing values of both d_D/e_D and b_C/e_C. Note that (i) in all cases the maximum value of G is at zero, indicating that the solutions drawn in Fig. 4 are EVSE candidates, and (ii) the graphs become steeper as the parameter ratios increase.

ducer (Fig. 4B), at the expense of ever decreasing density of nutrients (Fig. 4A), with eventual destruction of its ability to co-exist at EVSE. Note that there is an 'optimal' consumer efficiency where the density of the decomposer is maximized. Therefore, it does not necessarily follow that an efficient consumer (one that returns much of its energy and nutrients to the decomposers as opposed to exporting it from the ecosystem) always results in a higher density of decomposers.

The theory, therefore, predicts that ecosystems (at EVSE) with consumers that cause fast recycling of nutrients with little losses from the ecosystem should have a low density of consumers and nutrients and a high density of producers, compared to similar ecosystems but with slow nutrient cycling consumers. Thus, at EVSE, producers appear to 'benefit' from a fast recycling of nutrients through the consumers and at the expense of the consumers. Furthermore, such trends may not be sensitive to the efficiency with which decomposers cycle nutrients through the ecosystem. Thus, when the effects of nutrient recycling by both the producers and the consumers are combined, one gets the quadratic EVSE sensitivity (to efficiencies) surface of the decomposer densities (Fig. 4D). No such effect exists in the absence of a consumer (Fig. 2C).

The conclusion that consumers cannot be too efficient in cycling nutrients when the ecosystem is at its EVSE corresponds to the finding that large herbivores lose as much energy through respiration and other metabolic processes as they return to the ecosystem, primarily due to the indigestibility of their food (Schwartz and Hobbs, 1985; Renecker and Hudson, 1988; Moen *et al.*, 1996).

As the efficiencies of both D and C increase in re-cycling nutrients, the adaptive landscape becomes steeper (Fig. 5). Using the chain of reasoning in the previous section, the theory predicts that ecosystems with inefficient decomposers and consumers can potentially support more species than those with more efficient ones. In other words, a system with more open (less efficient) compartments will be more species-rich at EVSE compared with a more closed (more efficient) system. One must keep in mind that we use efficiency here in a special sense: a more efficient consumer, for example, is one that returns a larger proportion of its nutrients and energy to the ecosystem than a less efficient consumer. This is why we call it the 'ecosystem perspective efficiency'.

Because we are dealing with a differential game setting, one way to verify that candidate EVSE solutions are indeed an EVSE is, as discussed above, to 'play' the right number of coalition species, with their ESS values against a mutant species (a species with strategy values other than ESS). If the candidate solution is an EVSE, then numerical simulations of the system dynamics (equations 14 and 15 with the additional non-coalition species) should result in the mutant species eventually becoming extinct; that is, its density should go to zero, as required by equation 2. In all of our simulations, the mutants did become extinct.

THE ECOSYSTEM WITH TWO PRODUCERS AND ONE CONSUMER AT CANDIDATE ESS SOLUTIONS

Next, we attempted to solve for EVSE using the parameter values as in equation (19), but with $\rho = 2$ in equation (15). No ranges of parameter ratios for the efficiency of D and C resulted in EVSE candidates. Thus, for the given parameter values, no consumer can co-exist with two producers. However, when we chose $\sigma_m = 10$, we generated the sensitivity surfaces shown in Fig. 6. The parameter σ_m (equation 14) expresses the sharpness of the

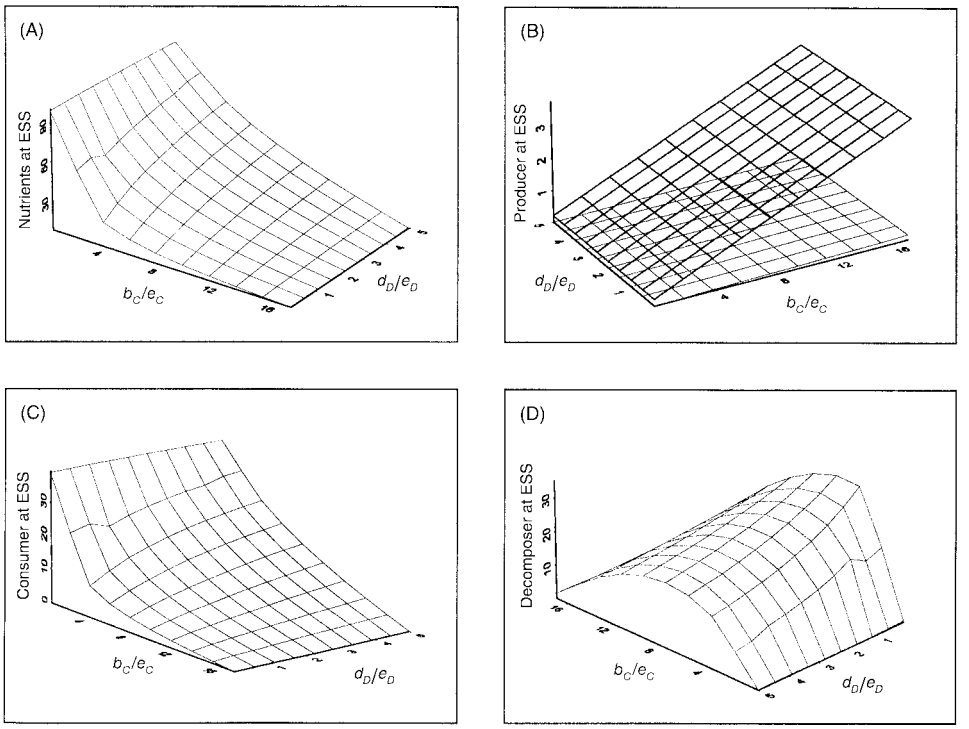

Fig. 6. EVSE candidate solutions for the ecosystem with two producers and one consumer (equation 15), and with parameter values and ranges given in equation (19), except for $\sigma_m = 10$. In (B), the lower surface represents x_1 and the upper surface represents x_2.

competition function $m(u, u_i)$ around the yet to be determined value of the ESS, u_i*. The larger the value of σ_m, the smaller the reduction in the competitive effect due to deviation of a strategy value from its corresponding ESS value (i.e. larger σ_m correspond to a flatter shape of the competition function). Since the value of competition is subtracted from the fitness of a species (equation 16), larger σ_m translates to smaller decreases in fitness when the strategy value u deviates from its ESS value. The fact that only one species can co-exist at candidate ESS solutions when $m(u, u_i)$ is flat, and two when it is sharp ($\sigma_m = 50$ *vs* 10), indicates that, in ecosystems where deviation from ESS values do not result in large reductions in fitness, fewer species co-exist at EVSE.

The sensitivity surfaces (of the densities of N, x_1, x_2, C and D) to the parameter values given in equation (19), but with $\sigma_m = 10$, are shown in Fig. 6 and the resulting G-functions for selected combinations of parameter ratios (d_D/e_D versus b_C/e_C) are shown in Fig. 7. Because all maxima of G are zero, and all real parts of the eigenvalues of **D** were negative, the surfaces represent candidate EVSE solutions. Furthermore, simulations (as described above) indicated that these are indeed EVSE solutions.

Note that the sensitivities in qualitative terms (i.e. directions and tilt of surfaces, and the range of parameter ratios for which N, x_1, x_2, C and D are positive) remain similar to those we found for the system with one producer and one consumer (Fig. 5). For example, both systems with one and two producers and a consumer exhibit the quadratic surface for D.

It is interesting to note that the species with lower densities at candidate EVSE solutions (x_1) is the species that is more efficient in cycling nutrients through the ecosystem (Table 1). For all ranges of parameter ratios (d_D/e_D versus b_C/e_C), the values of the ESS remained constant (to second decimal digit); therefore, the values in Table 1 did not change. As in the case for a system with one producer and one consumer, low consumer and decomposer efficiencies allow for potentially more species to co-exist at or near EVSE solutions (Fig. 7).

The values in Table 1 for the system with two producers and one consumer at EVSE are instructive. For producer 1, the input rate from the nutrient pool (N), the output rate to the consumer (C) and the decay rate (output to D) are all higher (per kg density) than for producer 2. For the 'faster' producer species ($i = 1$), the intra-specific competition is stronger

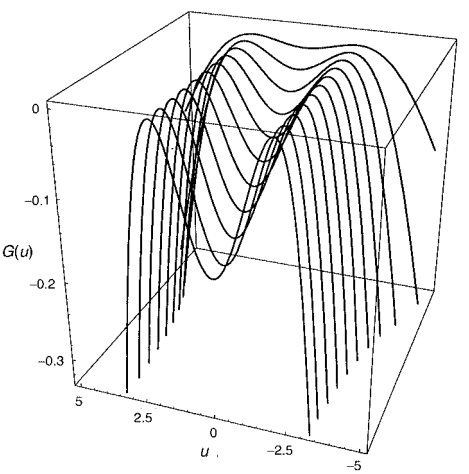

Fig. 7. A stack of $G(u)$ for the system with two producers and one consumer, and the parameter values given in equation (19), except for $\sigma_m = 10$. Each graph is drawn for a point on the mesh d_D/e_D versus b_C/e_C shown in Fig. 6. The graphs are drawn from back to front for increasing values of both d_D/e_D and b_C/e_C. Note that (i) in all cases the maximum value of G is at zero, indicating that the solutions drawn in Fig. 5 are EVSE candidates, and (ii) the graphs become steeper as the parameter ratios increase.

Table 1. Results from candidate EVSE solutions for a model ecosystem with two producers ($i = 1, 2$) and one consumer[a]

Function	$u_1^* = -1.93$	$u_2^* = 2.05$	Comments
$(b(u) + c(u))/e(u)$	51.69	50.68	Efficiency of producer i in cycling nutrients
$a(u)$	1.86	1.84	Input to producer i
$b(u)$	0.93	0.92	Output from producer i to decomposer
$c(u)$	4.64	4.60	Output from producer i to consumer
$e(u)$	0.09	0.09	Output from the ecosystem from producer i
$m(u_1, u_i)$	3.99	3.98	Competitive effect of producer i on producer 1
$m(u_2, u_i)$	38.42	3.99	Competitive effect of producer i on producer 2

[a] See equation (15) and parameter values in equation (19) with $\sigma_m = 10$.

than the inter-specific competition ($3.99 > 3.98$). For the 'slower' producer ($i = 2$), the reverse is true ($38.42 > 3.99$), and the strength of the intra-specific competition for both species is equal to the 15th decimal digit (3.99). The competitive effect of producer 1 on producer 2 (38.42) is larger than that of producer 2 on producer 1 (3.98). This compensates for the fact that species 1 is preferred by the consumer. Note that the biomass density of species 1 is lower than that of species 2 for the entire range of parameter sensitivities (Fig. 6B). Thus, without its competitive advantage over species 2, it is doubtful that the first consumer (species 1) would be able to co-exist at the candidate EVSE solutions. In fact, based on the sensitivity analysis and the simulation runs (of consumer species with strategy values other than the candidate ESS 'playing' against the ESS values), we have strong indications that the candidate EVSE solutions are unique. In other words, different strategy values simply cannot emerge for the candidate EVSE solutions. Finally, the biomass density of species 1 is lower than that of species 2 for the entire range of parameter sensitivities (Fig. 6B).

These results are interesting for two reasons. First, the results are consistent for the entire range for the parameter sensitivity. This is the range for which EVSE solutions actually exist. Second, the trends in the values of these functions (Table 1) are what we expect from empirical results (see discussion above): Much like deciduous and coniferous plant species in the boreal forest subject to foraging by moose (e.g. *Populus tremuloides* and *Picea glauca*), the 'efficient' species (*P. tremuloides*) circulates energy faster, is preferred by mammalian herbivores, its biomass density is smaller at the later stages of succession, the competitive effect of *P. tremuloides* on *P. glauca* is presumably stronger, primarily because of the former's faster growth rate, and its decay rate is faster compared to the less 'efficient' species (*P. glauca*). Yet, because of its high biomass, the total contribution of the less efficient producer to energy flow in the system at ECSE and EVSE is higher than that of the efficient producer. Note that these results are achieved without imposing diet preference on the consumer. With such preference, the trends (Table 1) will be even more pronounced. It should be emphasized that we are not claiming that the specific example we compare the results to – a boreal forest, in its later seral stages, and moose foraging – is anywhere near EVSE. In general, EVSE should be viewed as an idealized state that evolving ecological systems may or may not achieve. EVSE can be viewed as an attractor towards which ecosystems are evolving.

STRATEGY DYNAMICS

Equation (11) describes the dynamics of the strategy. The interest in this section revolves around the consequences of a fluctuating input Q to the nutrient compartment N (Fig. 1). In many ecosystems, these fluctuations are regular. Other regularly oscillating inputs to ecosystems are temperature (daily and yearly), incident light (daily and yearly), and so on. Because we have a driven system, at least in the neighbourhood of $\mathbf{u}^*$ and $\mathbf{x}^*$, the system variables (strategies and densities) should fluctuate with the same frequency as the input. One would then expect the strategy or some of its manifestations to fluctuate regularly. One consequence of the model is that there are likely to be phase shifts (but not frequency shifts) in the fluctuations of any of the system's state variables. For a system with nutrients, one producer species ($\sigma = 1$), decomposer and strategy (i.e. with no consumer (C) and with one producer species in equation 15), we chose the parameters as shown in equation (18). Except that now Q is

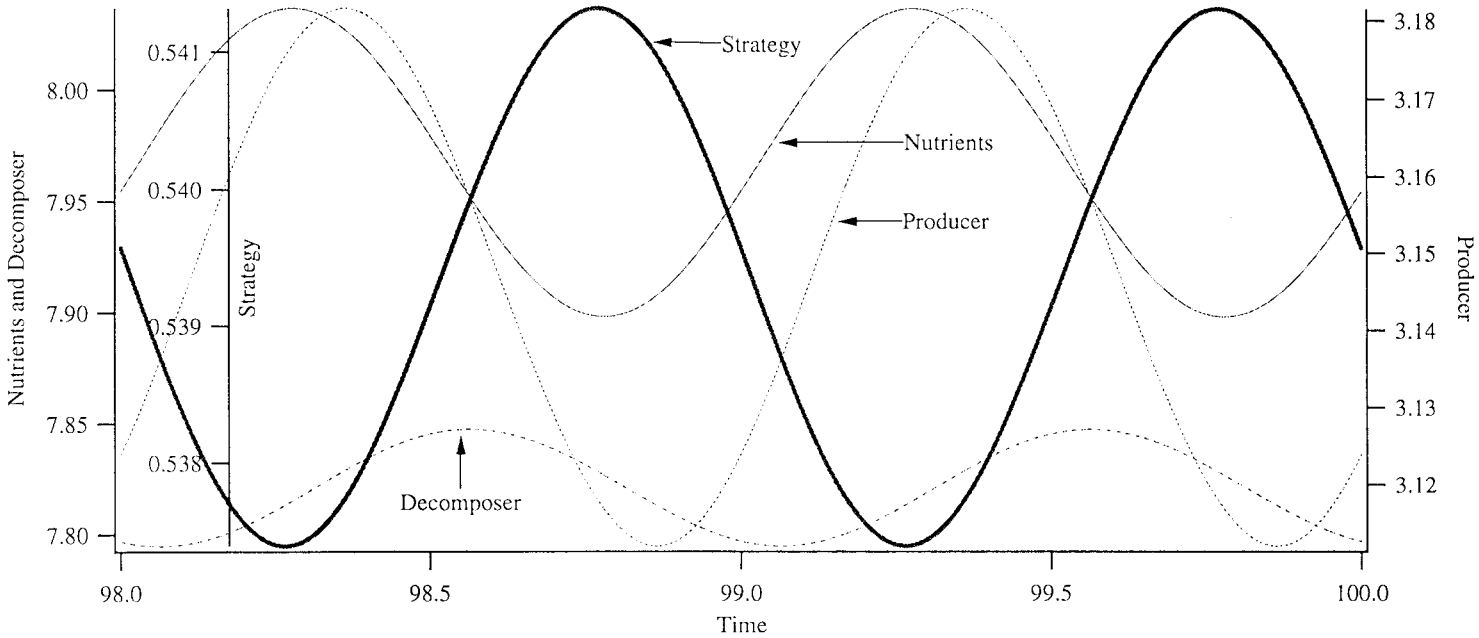

Fig. 8. Strategy dynamics (bold line) and the density of nutrients, producer and decomposer in a model ecosystem with no consumer.

$$Q(t) = A + B\sin(2\pi t/T) \tag{20}$$

where $A = 50$, $B = 1$ and $T = 1$. We also chose $h\sigma^2 = 10$ in equation (11). With these parameters, we integrated equations (12) and (15) (Fig. 8). Using the density of nutrients as a baseline, the model exhibits a phase shift in the density of producer and a further shift in the density of decomposer. These shifts are, of course, a direct consequence of the mathematics of the model, and if one is willing to lend some credence to the ecosystem model, then they should be expected in Nature as well.

The largest shift in phase occurs for the fluctuations in strategy value (Fig. 8). With the understanding that the strategy is some phenotypic trait, it is not difficult to see how strategy can fluctuate. Spectacular examples cover a spectrum of scales in Nature, from bird migration and deciduous trees to heart rate and hormonal changes. It is interesting to note that the strategy's phase is delayed by slightly less than 2π; for example (speculatively), a bear goes into hibernation slightly before the onset of winter, and trees shed leaves earlier than their physiological limitations might occur.

Next, we implemented the model with the parameter values that require two producers when a consumer is present (equation 18 but with $\sigma_m = 10$ and $Q(t)$ as in equation 20) (Fig. 9). Here, we get both strategies out of phase (by almost 2π radians). Strategy 1 was with a small phase shift compared to the rest of the system. It was the strategy of the second producer (the 'slow' producer) that lagged most.

CONCLUSIONS

Based on the sensitivity analysis of the flow rates in the ecosystem configurations we examined, we reached the following conclusions. In general, unless cycling efficiency of both the consumer and the decomposer are low, one would expect the presence of a consumer to increase the flow rate through the ecosystem. This is in contrast to our finding for systems at ECSE (Pastor and Cohen, 1997), where the presence of a consumer always

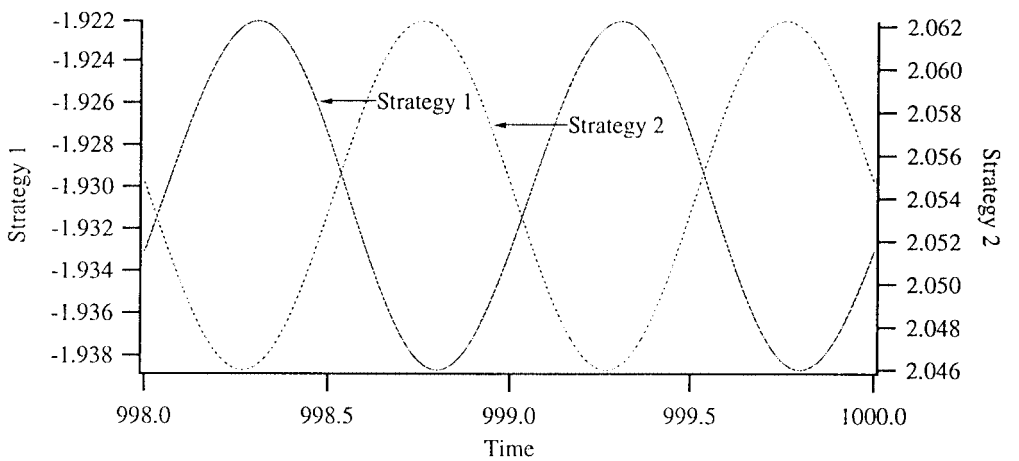

Fig. 9. Strategy dynamics for an ecosystem model with nutrients, two producers, one consumer and a decomposer.

decreased flows. The difference between ECSE and EVSE solutions is, of course, that some of the rate parameters in ECSE ecosystems are functions (of the strategy) in co-evolving ecosystems (i.e. observe the parameters in equation 12 that are being replaced by the functions in equations 14 and 15), and an optimal solution is derived in a game theoretic sense (all producers compete, both intra- and inter-specifically, while maximizing their fitness simultaneously).

The ecosystem model we analyse here is simple. Without including co-evolution, we previously used the model (Fig. 1 and equation 12) to capture two essential facts that were not included in the model analysed by Loreau (1995): (i) the consumer has a choice; (ii) one of the dietary items is of higher nutritional value than the other, and this item also decays faster and draws nutrients from the nutrient pool faster (a common situation). With these two facts, we showed (Pastor and Cohen, 1997) that the presence of a consumer reduces the flow through ecologically stable ecosystem models for a wide range of parameter values. This may be because the addition of a trophic level (consumers), without adjustment of parameter values (through evolution and maximizing fitness), simply adds another channel through which nutrients and energy are lost from the ecosystem. When evolution is allowed (i.e. when parameter values are allowed to evolve), the evolutionarily stable ecosystem adjusts to increase flows when a consumer is added to the system. Furthermore, adding one more producer increases flows even further.

Of all the ecosystem compartments, the decomposer displays the most interesting sensitivity surface in our model. While other compartments respond exponentially to changes in some parameter (efficiency) values (Figs 4A, B and C and 7A, B and C), the decomposer's surface is quadratic. There is some range of cycling efficiency of the consumer that maximizes the density of the decomposer when a consumer is present (Figs 4D and 7D). Even in an ecosystem without the consumer, the qualitative sensitivity of the decomposer density to changes in cycling efficiency is different to that of the other model compartments (compare Figs 2A and B with Fig. 2C).

We do not claim that EVSE itself is common; it may be viewed as some theoretical set of conditions that ecosystems (and co-evolving plant and animal communities) evolve towards. The dynamics of the evolutionary strategies (i.e. how EVSE is reached) is of much interest: one may find, for example, ESS strategy values that cycle, as opposed to fixed points, or even behave chaotically (Cohen and Vincent, 1997). The rate at which a system approaches EVSE is proportional to the gradient of the *G*-function (Vincent *et al.*, 1993; Cohen and Vincent, 1997). This means that, in our examples (Figs 3, 5 and 8), ratios of nutrient flows into and out of various compartments determine not only the value and existence of ESS, but also the rate at which EVSE is achieved.

When dynamics were added to the system, a whole host of new results became possible. In particular, with fluctuating inputs all state variables (densities and strategies) fluctuate at the same frequencies, but with different phase shifts. When the strategy relates to resource (nutrient) exploitation efficiency, phase shifts allow co-existence with species exploiting more of the resource at different times. Of course, all of these results are consequences of the model, and these phase shifts could be analysed in detail using transfer function methods (Grantham and Vincent, 1993). Our point here is that, in many evolutionary and population ecology models, the input to (and output from) the system are not considered explicitly. These so-called forcings can have simple and often easy to explain consequences.

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