Spatial Price Equilibrium and Food Webs: The Economics of Predator-Prey Networks

Proceedings of the
2011 IEEE International Conference on Supernetworks and System Management
F.-Y. Xu and J. Dong, Editors, IEEE Press, Beijing, China, pp 1-6.

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***Abstract*—In this paper, we prove that the equilibrium of predator-prey networks is, in fact, a spatial price equilibrium. This result demonstrates the underlying economics of predator-prey relationships and interactions and provides a foundation for the formulation and analysis of complex food webs, which are nature's supply chains, through the formalism of network equilibrium. Moreover, it rigorously links the equilibrium conditions of commodity networks in which a product is produced, transported, and consumed, with those of ecological networks in which prey are consumed by predators.**

***Index Terms*—spatial price equilibrium, supply chains, food webs, predator prey models, food chains, networks, network economics, economics of biological systems, ecological networks, network equilibrium, regional science, operations research, transportation, supernetworks**

I. Introduction

Equilibrium is a central concept in numerous disciplines from economics and regional science to operations research / management science and even in ecology and biology. Examples of specific equilibrium concepts include the well-known Walrasian price equilibrium in economics, Wardropian (traffic network) equilibrium in transportation science, and Nash equilibrium in game theory [1]. In ecology, equilibrium is in concert with the *balance of nature*, in that, since an ecosystem is a dynamical system, we can expect there to be some persistence or homeostasis in the system [2], [3], [4]. Moreover, equilibrium serves as a valuable paradigm that assists in the evaluation of the state of a complex system.

Equilibrium, as a concept, implies that there is more than a single decision-maker or agent, who, typically, seeks to optimize, subject to the underlying resource constraints. Hence, the formulation, analysis, and solution of such problems may be challenging. Notable methologies that have been developed over the past several decades that have been successfully applied to the analysis and computation of solutions to a plethora of equilibrium problems include variational inequality theory and the accompanying theory of projected dynamical systems ([1], [5] and the references therein).

Fascinatingly, it has now been recognized that numerous equilibrium problems as varied as the classical Walrasian price equilibrium problem, the classical oligopoly problem, the portfolio optimization problem, and even migration problems [6], which in their original formulations did not have a network structure identified, actually possess a network structure. In addition, such well-recognized network equilibrium problems as traffic network equilibrium problems with applications to congestion management on urban roads as well as to air traffic, and even to the Internet [7], as well as spatial price equilibrium problems, ([8], [9], [10]) also have an underlying network structure (with nodes corresponding to locations in space). Furthermore, it has now been established, through the supernetwork [11] formalism that even supply chain network problems, in which decision-makers (be they manufacturers, retailers, or consumers at demand markets) compete across a tier, but necessarily cooperate (to various degrees) between tiers, can be reformulated and solved as (transportation) network equilibrium problems. The same holds for complex financial networks with intermediaries [12]. In addition, the supernetwork framework has even been applied to the integration of social networks with supply chains [13] and with financial networks [14].

Hence, it is becoming increasingly evident that seemingly disparate equilibrium problems, in a variety of disciplines, can be uniformly formulated and studied as network equilibrium problems. Such identifications allow one to:
1. graphically visualize the underlying structure of systems as networks;
2. avail oneself of existing frameworks and methodologies for analysis and computations, and
3. gain insights into the commonality of structure and behavior of disparate complex systems that underly our economies and societies.

Nevertheless, although deep connections and equivalences have been made (and continue to be discovered) between/among different systems through the (super)network formalism, the systems studied, to-date, have been exclusively

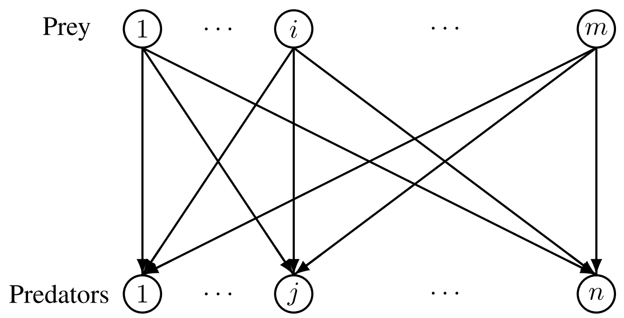

Fig. 1. The bipartite network with directed links representing the predator-prey problem

of a socio-technical-economic variety.

In this paper, we take on the challenge of proving the equivalence between ecological food webs and spatial price equilibrium problems; thereby, providing a foundation for the unification of these disparate systems and, in a sense, we bring the fields of economics (and operations research and regional science) closer to ecology (and biology).

This paper is organized as follows. In Section II, we briefly recall the predator-prey model of [4], which serves as the basis for the equivalence. In Section III, we establish the equivalence between predator-prey equilibrium and spatial price equilibrium. In Section IV, we develop extensions and propose a dynamic adjustment process, along with stability analysis results. Section V presents numerical examples, whereas Section VI contains a summary and suggestions for future research.

II. The Predator-Prey Model

In this Section, we briefly review the predator-prey model [4], whose structure is given in Figure 1. We consider an ecosystem in which there are m distinct types of prey and n distinct typed of predators with a typical prey species denoted by i and a typical predator species denoted by j. The biomass of a species i is denoted by B_i; $i = 1, \ldots, m$. E_i denotes the inflow (energy and nutrients) of species i with the autotroph species, that is, the prey, in Figure 1, having positive values of E_i; $i = 1, \ldots, m$, whereas the predators have $E_j = 0$; $j = 1, \ldots, n$. The parameter γ_i denotes the trophic assimilation efficiency of species i and the parameter μ_i denotes the coefficient that relates biomass to somatic maintenance. The variable X_{ij} is the amount of biomass of species i preyed upon by species j and we are interested in determining their equilibrium values for all prey and predator species pairs (i, j).

The prey equations that must hold are given by:

$$\gamma_i E_i = \mu_i B_i + \sum_{j=1}^{n} X_{ij}, \quad 1, \ldots, m. \tag{1}$$

Equation (1) means that for each prey species i, the assimilated biomass must be equal to its somatic maintenance plus the amount of its biomass that is preyed upon.

The predator equations, in turn, are given by:

$$\gamma_j \sum_{i=1}^{m} X_{ij} = \mu_j B_j, \quad j = 1, \ldots, n. \tag{2}$$

Equation (2) signifies that for each predator species j, its assimilated biomass is equal to its somatic maintenance (which is represented by its coefficient μ_j times its biomass).

Equations (1) and (2) may be interpreted as the conservation of flow equations, in network parlance, from a biomass perspective.

In addition, there is a parameter $\phi_{ij}; 1, \ldots, m; j = 1, \ldots, n$, which reflects the distance (note the spatial component) between distribution areas of prey i and predator j, with this parameter also capturing the transaction costs associated with handling and ingestion.

According to [4], the predation cost between prey i and predator j, denoted by F_{ij}, is given by:

$$F_{ij} = \phi_{ij} - \kappa_i B_i + \lambda_j B_j, \quad i = 1, \ldots, m; j = 1, \ldots, n, \tag{3}$$

where $-\kappa_i B_i$ represents the easiness of predation due to the abundance of prey B_i and $\lambda_j B_j$ denotes the intra-specific competition of predator species j. We group the species biomasses and the biomass flows intro the respective $m + n$ and mn dimensional vectors B^* and X^*.

Definition 1: Predator-Prey Equilibrium Conditions
A biomass and flow pattern (B^*, X^*), satisfying constraints (1) and (2), is said to be in equilibrium if the following conditions hold for each pair of prey and predators (i, j); $i = 1, \ldots, m$; $j = 1, \ldots, n$:

$$F_{ij} \begin{cases} = 0, & \text{if} \quad X^*_{ij} > 0, \\ \geq 0, & \text{if} \quad X^*_{ij} = 0. \end{cases} \tag{4}$$

These equilibrium conditions reflect that, if there is a biomass flow from i to j, then there is an *economic* balance between the advantages ($\kappa_i B_i$) and the inconveniences of predation ($\phi_{ij} + \lambda_j B_j$).

Observe that, in view of (1), (2), and (3), we may write $F_{ij} = F_{ij}(X)$, $\forall i, j$.

Clearly, the predator-prey equilibrium conditions (4) may be formulated as a variational inequality problem, as given below.

Theorem 1: Variational Inequality Formulation of Predator-Prey Equilibrium
A biomass flow pattern $X^* \in R^{mn}_+$ is an equilibrium according to Definition 1 if and only if it satisfies the variational inequality problem:

$$\sum_{i=1}^{m} \sum_{j=1}^{n} \left[\frac{\kappa_i}{\mu_i} \sum_{j=1}^{n} X^*_{ij} - \frac{\kappa_i}{\mu_i} \gamma_i E_i + \phi_{ij} + \frac{\lambda_j \gamma_j}{\mu_j} \sum_{i=1}^{m} X^*_{ij} \right]$$

$$\times \left[X_{ij} - X^*_{ij} \right] \geq 0, \quad \forall X \in R^{mn}_+. \tag{5}$$

Proof: Note that, by making use of (1), (2), and (3):

$$F_{ij}(X) = \frac{\kappa_i}{\mu_i} \sum_{j=1}^{n} X_{ij} - \frac{\kappa_i}{\mu_i}\gamma_i E_i + \phi_{ij} + \frac{\lambda_j \gamma_j}{\mu_j} \sum_{i=1}^{m} X_{ij}. \quad (6)$$

We first establish necessity. From (4) we have that

$$\left[\frac{\kappa_i}{\mu_i} \sum_{j=1}^{n} X^*_{ij} - \frac{\kappa_i}{\mu_i}\gamma_i E_i + \phi_{ij} + \frac{\lambda_j \gamma_j}{\mu_j} \sum_{i=1}^{m} X^*_{ij} \right] \times \left[X_{ij} - X^*_{ij} \right] \geq 0, \quad \forall X_{ij} \geq 0, \quad (7)$$

since, indeed, if $X^*_{ij} > 0$, then the left-hand-side of inequality (7) prior to the multiplication sign is zero, since the equilibrium conditions (4) are assumed to hold, and, hence, the inequality in (7) holds; on the other hand, if $X^*_{ij} = 0$, then both the expression before the multiplication sign in (7) (due to the equilibrium conditions) is nonnegative as is the one after the multiplication sign (due to the assumption of the nonnegativity of the biomass flows), and the result in (7) also follows. Summing now (7) over all prey species i and over all predator species j yields the variational inequality (5).

In order to prove sufficiency, we proceed as follows. Assume that variational inequality (5) holds. Set $X_{kl} = X^*_{kl}$ for all $kl \neq ij$ and substitute into (5), which yields:

$$\left[\frac{\kappa_i}{\mu_i} \sum_{j=1}^{n} X^*_{ij} - \frac{\kappa_i}{\mu_i}\gamma_i E_i + \phi_{ij} + \frac{\lambda_j \gamma_j}{\mu_j} \sum_{i=1}^{m} X^*_{ij} \right] \times \left[X_{ij} - X^*_{ij} \right] \geq 0, \quad \forall X_{ij} \geq 0, \quad (8)$$

from which equilibrium conditions (4) follow with note of (6).

III. The Equivalence Between Predator Prey Problems and Spatial Price Equilibria

As noted in [1], the concept of a network in economics was implicit as early as in the classical work of Cournot [15], who not only seems to have first explicitly stated that a competitive price is determined by the intersection of supply and demand curves, but had done so in the context of two spatially separated markets in which the cost of transporting the good between markets was considered.

Samuelson [8] provided a rigorous mathematical formulation of the spatial price equilibrium problem and explicitly recognized and utilized the network structure, which was bipartite. In spatial price equilibrium problems, unlike classical transportation problems, the supplies and the demands are variables, rather than fixed quantities. The work was subsequently extended by [9] and others (cf. [16], [17], [10], [1], and the references therein) to include, respectively, multiple commodities, and asymmetric supply price and demand functions, as well as other extensions, made possible by such advances as quadratic programming techniques, complementarity theory, as well as variational inequality theory (which allowed for the formulation and solution of equilibrium problems for which no optimization reformulation of the governing equilibrium conditions was available).

We now briefly recall the spatial price equilibrium problem. For a variety of spatial price equilibrium models, we refer the interested reader to [1]. There are m supply markets and n demand markets involved in the production / consumption of a homogeneous commodity. Denote a typical supply market by i and a typical demand market by j. Let s_i denote the supply of the commodity associated with supply market i and let π_i denote the supply price of the commodity associated with supply market i. Let d_j denote the demand associated with demand market j and let ρ_j denote the demand price associated with demand market j. Group the supplies into the vector $s \in R^m$ and the demands into the vector $d \in R^n$.

Let Q_{ij} denote the nonnegative commodity shipment between the supply and demand market pair (i, j) and let c_{ij} denote the nonnegative unit transaction cost associated with trading the commodity between (i, j). Assume that the transaction cost includes the cost of transportation. Group the commodity shipments into the vector $Q \in R^{mn}_+$.

The following feasibility (conservation of flow) equations must hold: for every supply market i and each demand market j:

$$s_i = \sum_{j=1}^{n} Q_{ij}, \quad i = 1, \ldots, m, \quad (9)$$

and

$$d_j = \sum_{i=1}^{m} Q_{ij}, \quad j = 1, \ldots, n. \quad (10)$$

Equations (9) and (10) reflect that the markets clear and that the supply at the supply market is equal to the sum of the commodity flows to all the demand markets. Also, the demand at each demand market must be satisfied by the sum of the commodity shipments from all the supply markets.

Definition 2: Spatial Price Equilibrium
The spatial price equilibrium conditions, assuming perfect competition, take the following form: for all pairs of supply and demand markets $(i, j) : i = 1, \ldots, m; j = 1, \ldots, n$:

$$\pi_i + c_{ij} \begin{cases} = \rho_j, & \text{if} \quad Q^*_{ij} > 0 \\ \geq \rho_j, & \text{if} \quad Q^*_{ij} = 0. \end{cases} \quad (11)$$

The spatial price equilibrium conditions (11) state that if there is trade between a market pair (i, j), then the supply price at supply market i plus the unit transaction cost between the pair of markets must be equal to the demand price at demand market j in equilibrium; if the supply price plus the transaction cost exceeds the demand price, then there will be no shipment between the supply and demand market pair. Let K denote the closed convex set where $K \equiv \{(s, Q, d) | Q \geq 0, (9) \text{ and } (10) \text{ hold}\}$.

The supply price, demand price, and transaction cost structures are now discussed. Assume that, for the sake of generality, the supply price associated with any supply market may depend upon the supply of the commodity at every supply market, that is,

$$\pi_i = \pi_i(s), \quad i = 1, \ldots, m, \quad (12)$$

where each π_i is a known continuous function.

Similarly, the demand price associated with a demand market may depend upon, in general, the demand of the commodity at every demand market, that is,

$$\rho_j = \rho_j(d), \quad j = 1, \ldots, n, \tag{13}$$

where each ρ_j is a known continuous function.

The unit transaction cost between a pair of supply and demand markets may, in general, depend upon the shipments of the commodity between every pair of markets, that is,

$$c_{ij} = c_{ij}(Q), \quad i = 1, \ldots, m; j = 1, \ldots, n, \tag{14}$$

where each c_{ij} is a known continuous function.

In the special case where the number of supply markets m is equal to the number of demand markets n, the transaction cost functions (14) are assumed to be fixed, and the supply price functions and demand price functions are symmetric, i.e., $\frac{\partial \pi_i}{\partial s_k} = \frac{\partial \pi_k}{\partial s_i}$, for all $i = 1, \ldots, n$; $k = 1, \ldots, n$, and $\frac{\partial \rho_j}{\partial d_l} = \frac{\partial \rho_l}{\partial d_j}$, for all $j = 1, \ldots, n$; $l = 1, \ldots, n$, then the above model with supply price functions (12) and demand price functions (13) collapses to a class of single commodity models introduced in [9] for which an equivalent optimization formulation exists.

We now present the variational inequality formulation of the equilibrium conditions (11).

Theorem 2: Variational Inequality Formulation of Spatial Price Equilibrium

A commodity production, shipment, and consumption pattern $(s^*, Q^*, d^*) \in K$ *is in equilibrium according to Definition 2 if and only if it satisfies the variational inequality problem:*

$$\sum_{i=1}^{m}\sum_{j=1}^{n} \pi_i(s^*) \times (s_i - s_i^*) + \sum_{i=1}^{m}\sum_{j=1}^{n} c_{ij}(Q^*) \times (Q_{ij} - Q_{ij}^*)$$
$$- \sum_{j=1}^{n} \rho_j(d^*) \times (d_j - d_j^*) \geq 0, \quad \forall (s, Q, d) \in K. \tag{15}$$

Proof: See [1].

We now establish our main result.

Theorem 3: Equivalence Between Predator-Prey Equilibria and Spatial Price Equilibria

An equilibrium biomass flow pattern satisfying equilibrium conditions (4) coincides with an equilibrium commodity shipment pattern satisfying equilibrium conditions (11).

Proof: We establish the equivalence by utilizing the respective variational inequalities (5) and (15). First, we note that (5) may be expressed as: determine $X^* \in R_+^{mn}$ such that

$$\sum_{i=1}^{m} \left[\frac{\kappa_i}{\mu_i} \sum_{j=1}^{n} X_{ij}^* - \frac{\kappa_i}{\mu_i}\gamma_i E_i \right] \times \left[\sum_{j=1}^{n} X_{ij} - \sum_{j=1}^{n} X_{ij}^* \right]$$
$$+ \sum_{i=1}^{m}\sum_{j=1}^{n} \phi_{ij} \times (X_{ij} - X_{ij}^*)$$
$$+ \left[\sum_{j=1}^{n} \frac{\lambda_j \gamma_j}{\mu_j} \sum_{i=1}^{m} X_{ij}^* \right] \times \left[\sum_{i=1}^{m} X_{ij} - \sum_{i=1}^{m} X_{ij}^* \right] \geq 0, \forall X \in R_+^{mn}. \tag{16}$$

Letting now:

$$Q_{ij} \equiv X_{ij}, \quad \forall i, j,$$

it follows then that $s_i = \sum_{j=1}^{n} Q_{ij} = \sum_{j=1}^{n} X_{ij}$ and $d_j = \sum_{i=1}^{m} Q_{ij} = X_{ij}$, for all i, j, in which case we may rewrite (16) as: determine $(s^*, Q^*, d^*) \in K$ such that

$$\sum_{i=1}^{m} \left[\frac{\kappa_i}{\mu_i} s_i^* - \frac{\kappa_i}{\mu_i}\gamma_i E_i \right] \times [s_i - s_i^*] + \sum_{i=1}^{m}\sum_{j=1}^{n} \phi_{ij} \times (Q_{ij} - Q_{ij}^*)$$
$$+ \sum_{j=1}^{n} \left[\frac{\lambda_j \gamma_j}{\mu_j} d_j^* \right] \times \left[d_j - d_j^* \right] \geq 0, \quad \forall (s, Q, d) \in K. \tag{17}$$

Letting now:

$$\pi_i(s) \equiv \frac{\kappa_i}{\mu_i} s_i - \frac{\kappa_i}{\mu_i}\gamma_i E_i, \quad i = 1, \ldots, m; \tag{18}$$

$$c_{ij}(Q) \equiv \phi_{ij}, \quad i = 1, \ldots, m; j = 1, \ldots, n; \tag{19}$$

and

$$\rho_j(d) \equiv -\frac{\lambda_j \gamma_j}{\mu_j} d_j, \quad j = 1, \ldots, n, \tag{20}$$

we conclude that, indeed, a biomass equilibrium pattern coincides with a spatial price equilibrium pattern.

The above equivalence provides a novel interpretation of the predator-prey equilibrium conditions in that there will be a positive flow of biomass/commodity from a supply market (prey species) to a demand market (predator species) if the supply price (or value of the biomass/commodity) plus the unit transaction cost is equal to the demand price that consumers (predators) are willing to "pay."

Interestingly, the predator-prey model on a bipartite network proposed by [4] is actually a classical one in that, from a spatial price equilibrium perspective, the supply price at a supply market depends only upon the supply of the commodity at the market; the same for the demand markets. Moreover, the unit transaction/transportation cost between a pair of supply and demand markets is assumed to be independent of the flow. Hence, for this specific food web model there is an optimization reformulation of the governing equilibrium conditions.

With the above connection, we can now transfer the numerous special-purpose algorithms that are available for the solution of spatial price equilibria, and which effectively exploit the underlying network structure, for the computation of predator prey biomass equilibria. Moreover, since spatial price equilibrium problems can be transformed into transportation network equilibrium problems [18] further theoretical and practical results can be expected.

For completeness, we now provide an alternative variational inequality to (15) which captures *product differentiation* in predator-prey networks. Specifically, we define differentiated demand price functions ρ_{ij}, which reflect the demand price associated with demand (predator) market j for supply (prey) market i, such that

$$\rho_{ij}(Q) \equiv -\frac{\lambda_j \gamma_j}{\mu_j} \sum_{i=1}^{m} Q_{ij} + \frac{\kappa_i}{\mu_i} \gamma_i E_i, \forall i, j. \quad (21)$$

The following result is immediate, with notice to (5), (21), and that $Q_{ij} \equiv X_{ij}$, $\forall i, j$, and with $\pi_i(s) \equiv \frac{\kappa_i}{\mu_i} s_i$, $\forall i$:

Corollary 1: Alternative Variational Inequality Formulation of Predator-Prey Equilibrium as a Network Equilibrium with Product Differentiation

An equilibrium biomass flow pattern satisfying equilibrium conditions (4) coincides with an equilibrium commodity shipment pattern with differentiated product prices with the variational inequality formulation: determine (s^*, Q^*) with $Q \in R_+^{mn}$ and (9) satisfied, such that

$$\sum_{i=1}^{m} \pi_i(s^*) \times [s_i - s_i^*]$$

$$+ \sum_{i=1}^{m} \sum_{j=1}^{n} [\phi_{ij} - \rho_{ij}(Q^*)] \times \left[Q_{ij} - Q_{ij}^*\right] \geq 0,$$

$$\forall (s, Q) \, \textit{such that} \, Q \in R_+^{mn} \, \textit{and} \, (9) \, \textit{holds}. \quad (22)$$

IV. Model Extensions

Through the equivalences established in Section III, many possibilities exist for extending the fundamental network economics model(s) of food webs (including the predator-prey model recalled in Section II) presented in [4]. Specifically, we propose that the unit transaction costs, the ϕ_{ij}s, need no longer be fixed, but can be flow-dependent, and monotone increasing, so that competition associated with foraging can also be captured. Of course, one may also generalize the corresponding biomass functions to correspond to nonlinear supply price and demand price functions and to also generalize the unit transaction cost functions to be nonlinear. Such general spatial price equilibrium models [1] already exist and the methodologies can then be applied to ecological predator prey network systems.

In addition, we believe that general food web models can be reformulated and solved as spatial price equilibrium problems on more general networks as in [10]. Finally, we note that, due to the variational inequality formulation (15), we may exploit the connection between sets of solutions to variational inequality problems and sets of stationary points of projected dynamical systems. In so doing, a natural dynamic adjustment process becomes:

$$\dot{Q}_{ij} = \max\{0, \rho_j(d) - c_{ij}(Q) - \pi_i(s))\}, \quad \forall i, j. \quad (23)$$

Letting $\hat{F}_{ij}$=$\pi_i(s) + c_{ij}(Q) - \rho_j(d)$, $\forall i, j$, we can write the following pertinent ordinary differential equation (ODE) for the adjustment process of commodity (biomass) shipments in vector form as [5]:

$$\dot{Q} = \Pi_K(Q, -\hat{F}(Q)), \quad (24)$$

where $\hat{F}$ is the vector with components $\hat{F}_{ij}$; $i = 1, \ldots, m$; $j = 1, \ldots, n$ and

$$\Pi_K(x, v) = \lim_{\delta \to 0} \frac{(P_K(x + \delta v) - x)}{\delta}, \quad (25)$$

where

$$P_K(x) = \arg\min_{z \in K} \|x - z\|. \quad (26)$$

We now present a stability result (see [5]) since, due to the equivalence established between the two network systems, its relevance to predator-prey problems is notable.

Theorem 4

Suppose that (s^*, Q^*, d^*) is a spatial price equilibrium according to Definition 2 and that the supply price functions π, the transaction cost functions c, and the negative demand price functions ρ are (locally) monotone, respectively, at s^*, Q^*, and d^*. Then (s^*, Q^*, d^*) is a globally monotone attractor (monotone attractor) for the adjustment process solving ODE (24).

Stronger results, including stability analysis results, can be obtained under strict as well as strong monotonicity of these functions, with the latter guaranteeing both existence and uniqueness of the solution (s^*, Q^*, d^*) to (15).

We exploit the above connection through our numerical procedure in the next section where we provide numerical examples.

Of course, a dynamic adjustment process, analogous to (23), can be constructed for variational inequality (22).

V. Numerical Examples

In this Section, we present several numerical examples. We used the Euler method, which is induced by the general iterative scheme of [19] and which has been applied to solve spatial price equilibrium problem as projected dynamical systems ([20], [5], where convergence results may also be found).

Specifically, one initializes the Euler method with an initial nonnegative commodity shipment pattern and then, at each iteration τ, one computes the commodity shipments for all pairs of supply and demand markets according to the formula:

$$Q_{ij}^{\tau+1} = \max\{0, a_\tau(\rho_j(d^\tau) - c_{ij}(Q^\tau) - \pi_i(s^\tau)) + Q_{ij}^\tau\}. \forall i, j \quad (27)$$

The algorithm was considered to have converged to a solution when the absolute value of each of the successive commodity shipment iterates differed by no more than $\epsilon = 10^{-5}$. We utilized the sequence $a_\tau = .1\{1, \frac{1}{2}, \frac{1}{2}, \ldots\}$, which satisfies the requirements for convergence of the Euler method. The Euler method was implemented in FORTRAN on a Linux-based computer system at the University of Massachusetts Amherst.

In order to appropriately depict the reality of predator-prey ecosystems, we utilized parameters, in ranges, as outlined in [4]. The computed equilibrium biomass flows for all the numerical examples are given in Table 1.

Example 1

TABLE I
EQUILIBRIUM SOLUTIONS FOR THE EXAMPLES

(i,j)	Q^*_{ij}	Example 1	Example 2	Example 3
$(1,1)$	Q^*_{11}	429.61	454.83	341.08
$(1,2)$	Q^*_{12}	110.81	122.85	332.97
$(1,3)$	Q^*_{13}	416.66	361.72	324.95
$(2,1)$	Q^*_{21}	405.34	246.49	332.73
$(2,2)$	Q^*_{22}	101.32	114.67	334.59
$(2,3)$	Q^*_{23}	407.62	496.85	331.18

This example consisted of two prey species and three predator species. The parameters for prey species 1 were: $\kappa_1 = .10$, $\mu_1 = .50$, and $\gamma_1 = 1.00$, with $E_1 = 1,000$. The parameters for prey species 2 were: $\kappa_2 = .10$, $\mu_2 = 1.00$, and $\gamma_2 = 1.00$, with $E_2 = 1,000$. These values resulted in supply price functions given by:

$$\pi_1 = .2s_1 - 100, \quad \pi_2 = .1s_2 - 100.$$

The unit transaction costs were:

$$\phi_{11} = .10, \quad \phi_{12} = .20, \quad \phi_{13} = .30,$$

$$\phi_{21} = .15, \quad \phi_{22} = .10, \quad \phi_{23} = .20.$$

The parameters for the predators were: for predator 1: $\lambda_1 = .02$, $\mu_1 = .20$, and $\gamma_1 = .10$; for predator 2: $\lambda_2 = .04$, $\mu_2 = .20$, and $\gamma_2 = .20$. The parameters for predator 3 were: $\lambda_3 = .02$, $\mu_3 = .2$, and $\gamma_3 = .1$.

These parameters resulted in demand price functions given by:

$$\rho_1 = -.01d_1, \quad \rho_2 = -.04d_2, \quad \rho_3 = -.01d_3.$$

The computed equilibrium commodity/biomass flow pattern is given in Table 1.

Example 2

The second example had the same data as Example 1 except that now we considered unit transaction cost functions that captured congestion (as in the model extension in Section IV). The unit transaction cost functions were now:

$$\phi_{11} = .01Q_{11}+.1, \quad \phi_{12} = .02Q_{12}+.2, \quad \phi_{13} = .01Q_{13}+.3,$$

$$\phi_{21} = .03Q_{21}+.15, \quad \phi_{22} = .04Q_{22}+.1, \quad \phi_{23} = .01Q_{23}+.2.$$

The computed solution is given in Table 1.

Example 3

Example 3 had the same supply price function and unit transaction cost data as Example 1 but here we considered the interesting scenario identified in [4] where $\lambda_j = 0.00$ for all predators j. This scenario results in all the demand price functions to be identically equal to 0.00. The computed solution for this example is also reported in Table 1.

VI. SUMMARY AND SUGGESTIONS FOR FUTURE RESEARCH

In this paper we established the equivalence between two network systems occurring in entirely different disciplines – in ecology (and biology) with economics (and operations research and regional science). In particular, we proved the equivalence of the governing equilibrium conditions of predator-prey systems with spatial price equilibrium problems through their corresponding variational inequality formulations. Through this connection, we then unveiled natural extensions of the basic bipartite predator-prey network model along with a dynamic adjustment process. We also presented an alternative variational inequality formulation using a product differentiation concept. We provided both theoretical results as well as numerical examples.

We can expect continuing research in network equilibrium models of complex food webs, nature's supply chains, in the future.

ACKNOWLEDGMENTS

The authors are grateful to the Engineering Computer Services at the University of Massachusetts Amherst for setting up Professor Anna Nagurney's Linux system, which was used for the numerical experiments. Support from the John F. Smith Memorial Fund is acknowledged for the purchase of this computer system.

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