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

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Background and Motivation

Equilibrium is a *central concept in numerous disciplines from economics and regional science to operations research / management science and even in ecology and biology*.

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 (Egerton (1973), Cuddington (2001), and Mullon, Shin, and Cury (2009)).

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 methodologies 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 *inequality theory and the accompanying theory of projected dynamical systems* (cf. Nagurney (1999) and Nagurney and Zhang (1996) and the references therein).

The Variational Inequality Problem

We utilize the theory of variational inequalities for the formulation, analysis, and solution of both centralized and decentralized network problems.

Definition: The Variational Inequality Problem

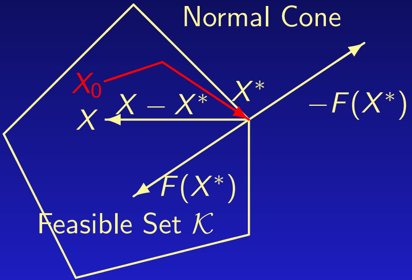
The finite-dimensional variational inequality problem, $\mathrm{VI}(F, \mathcal{K})$, is to determine a vector $X^* \in \mathcal{K}$, such that:

$$\langle F(X^*)^T, X - X^* \rangle \geq 0, \quad \forall X \in \mathcal{K},$$

where F is a given continuous function from $\mathcal{K}$ to R^N, $\mathcal{K}$ is a given closed convex set, and $\langle \cdot, \cdot \rangle$ denotes the inner product in R^N.

Geometric Interpretation of VI($F, \mathcal{K}$) and a Projected Dynamical System (Dupuis and Nagurney, Nagurney and Zhang)

In particular, $F(X^*)$ is "orthogonal" to the feasible set $\mathcal{K}$ at the point X^*.



Associated with a VI is a Projected Dynamical System, which provides the underlying dynamics to the equilibrium.

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 (cf. Nagurney (2003)), which in their original formulations did not have a network structure identified, *actually possess a network structure*.

Also, it has been established, *through the supernetwork (cf. Nagurney and Dong (2002)) formalism* that supply chain network problems, in which decision-makers (be they manufacturers, retailers, or even 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* (see Liu and Nagurney (2007)).

In addition, the supernetwork framework has even been applied to *the integration of social networks with supply chains* (see Cruz, Nagurney, and Wakolbinger (2006)) and *with financial networks* (cf. Nagurney, Wakolbinger, and Zhao (2006)).

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, to-date, have been exclusively of a socio - technical - economic variety*.

Here, 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, the fields of economics (and regional science) closer to ecology (and biology).

Supply Chains in Nature

The Predator-Prey Model

The Predator-Prey Network

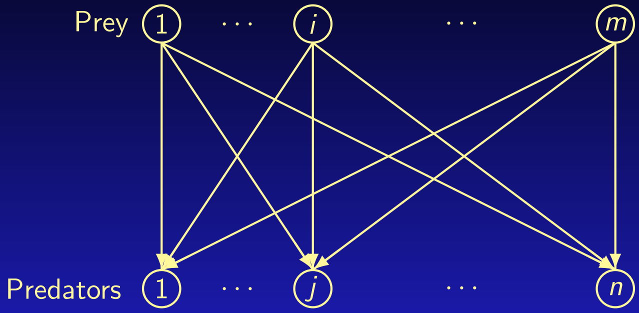


Figure 1: The bipartite network with directed links representing the predator-prey problem

We briefly review the predator-prey model (cf. Mullon, Shin, and Cury (2009)), 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).

In addition, there is a parameter ϕ_{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 Mullon, Shin, and Cury (2009), *the predation cost* between prey i and predator j, denoted by F_{ij}, is given by:

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

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 $F_{ij} = F_{ij}(X)$, $\forall i, j$.

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

Theorem 1

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:

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

$$\forall X \in R^{mn}_+. \qquad (5)$$

Proof: Note that

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

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

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

since, if $X_{ij}^* > 0$, then the left-hand-side of equation (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:

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

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

The Equivalence Between Predator-Prey Problems and Spatial Price Equilibria

The Spatial Price Equilibrium Problem

We now briefly recall the spatial price equilibrium problem. For a variety of spatial price equilibrium models, we refer the interested reader to Nagurney (1999).

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:

$$s_i = \sum_{j=1}^{n} Q_{ij} \tag{9}$$

and

$$d_j = \sum_{i=1}^{m} Q_{ij}. \tag{10}$$

Let K denote the closed convex set where $K \equiv \{(s, Q, d) | Q \in R_+^{mn} \text{ and } (9)\ (10) \text{ hold}\}$.

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 $(i,j) : i = 1, \ldots, m; j = 1, \ldots, n$*:*

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

These conditions are due to Samuelson (1952) and Takayama and Judge (1971).

The supply price associated with any supply market may depend upon the supply of the commodity at every supply market, that is,

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

where each π_i is a known continuous function.

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.

Theorem 2: Variational Inequality Formulation of Spatial Price Equilibrium

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

$$\sum_{i=1}^{m}\sum_{j=1}^{n}\pi_i(s^*)\times(s_i-s_i^*)+\sum_{i=1}^{m}\sum_{j=1}^{n}c_{ij}(Q^*)\times(Q_{ij}-Q_{ij}^*)$$

$$-\sum_{j=1}^{n}\rho_j(d^*)\times(d_j-d_j^*)\geq 0,\quad \forall(s,Q,d)\in K. \qquad (15)$$

We now state 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

$$\sum_{i=1}^{m}\left[\frac{\kappa_i}{\mu_i}\sum_{j=1}^{n}X^*_{ij}-\frac{\kappa_i}{\mu_i}\gamma_i E_i\right]\times\left[\sum_{j=1}^{n}X_{ij}-\sum_{j=1}^{n}X^*_{ij}\right]$$

$$+\sum_{i=1}^{m}\sum_{j=1}^{n}\phi_{ij}\times(X_{ij}-X^*_{ij})+\left[\sum_{j=1}^{n}\frac{\lambda_j\gamma_j}{\mu_j}\sum_{i=1}^{m}X^*_{ij}\right]\times\left[\sum_{i=1}^{m}X_{ij}-\sum_{i=1}^{m}X^*_{ij}\right]\geq 0, \tag{16}$$

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

$$\sum_{i=1}^{m} \left[\frac{\kappa_i}{\mu_i} s_i^* - \frac{\kappa_i}{\mu_i} \gamma_i E_i \right] \times [s_i - s_i^*] + \sum_{i=1}^{m} \sum_{j=1}^{n} \phi_{ij} \times (Q_{ij} - Q_{ij}^*)$$

$$+ \sum_{j=1}^{n} \left[\frac{\lambda_j \gamma_j}{\mu_j} d_j^* \right] \times \left[d_j - d_j^* \right] \geq 0, \quad \forall (s, Q, d) \in K. \qquad (17)$$

Letting now:

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

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

and

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

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."

We 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

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

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

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

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

Modeling Extensions and Dynamics

We exploit the connection between sets of solutions to variational inequality problems and sets of solutions to projected dynamical systems. In so doing, a natural dynamic adjustment process becomes:

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

Letting $\hat{F}_{ij} = \pi_i(s) + c_{ij}(Q) - \rho_j(d)$, $\forall i, j$, we can write the following pertinent ordinary dofferential equation (ODE) for the adjustment process of commodity (biomass) shipments in vector form as (see also Nagurney and Zhang (1996)):

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

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

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

where

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

A stability result (see Nagurney and Zhang (1996)):

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.

The Algorithm and Numerical Examples

We used the Euler method, which is induced by the general iterative scheme of Dupuis and Nagurney (1993) and which has been applied to solve spatial price equilibrium problem as projected dynamical systems (cf. Nagurney, Takayama, and Zhang (1997) and Nagurney and Zhang (1996), where convergence results may also be found).

The Euler method was initialized with a nonnegative commodity shipment pattern and then, at each iteration τ, we computed the commodity shipments for all pairs of supply and demand markets according to the formula:

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

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 computer system used was a Unix-based system at the University of Massachusetts Amherst. The Euler method was implemented in FORTRAN.

In order to appropriately depict reality of predator-prey ecosystems, we utilized parameters, in ranges, as outlined in Mullon, Shin, and Cury (2009). The computed equilibrium biomass flows for all the numerical examples are given in Table 1.

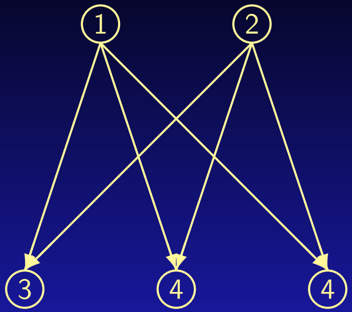


Figure 2: The network for the numerical examples

Example 1

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:

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

Examples 2 and 3

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 4). the unit transaction cost functions were now:

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

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

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 Mullon, Shin, and Cury (2009) 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 given in Table 1.

The computed solutions are given in Table 1.

The computed equilibrium commodity/biomass flow patterns for the examples.

Table 1: 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

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 regional science.

- 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 bipartite prey-predator network model, including a dynamic version.

- We provided both theoretical results as well as numerical examples.

- We can expect continuing research in network equilibrium models of complex food webs in the future.

THANK YOU!

For more information, see: http://supernet.som.umass.edu