

Dynamics and Equilibria of Ecological Predator-Prey Networks
as
Nature's Supply Chains

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February 2011; revised May 2011

Transportation Research E **48**: (2012), pp 89-99.

Abstract: In this paper, we develop a dynamic network model of ecological food webs and prove that the set of stationary points of the projected dynamical system coincides with the set of solutions of a variational inequality governing the equilibrium of predator-prey networks. We also establish the equivalence between the ecological models and supply chain network equilibrium models and highlight the connections to spatial price equilibrium problems. We propose an algorithmic scheme, provide convergence results, and apply it to a food web drawn from a fisheries application.

This paper is a contribution to the interdisciplinary supply chain network literature.

Key words: supply chains, food webs, predator-prey models, projected dynamical systems, variational inequalities, transportation and logistics, fisheries

1. Introduction

Competition is central not only to human interactions in economic systems but also to nature. Coupled with competition, is the construct of equilibrium, which provides a benchmark against which the state of a natural or economic system can be evaluated. For example, 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 (Odum (1971), Egerton (1973), Cuddington (2001), and Mullon, Shin, and Cury (2009)).

Equilibrium implies that there are multiple decision-makers or agents, who, typically, seek to optimize their decisions, subject to the underlying resource constraints, and who compete with one another until they cannot improve upon their situation through unilateral action. Although the formulation, analysis, and solution of such problems may be challenging, such notable methodologies as variational inequalities and projected dynamical systems have now been successfully applied for the analysis and computation of solutions to a plethora of equilibrium problems in transportation and logistics; economics and finance, and energy and the environment (cf. Nagurney (1999, 2006), Nagurney and Zhang (1996a), Zhang (2006), Yang and Zhang (2007), Nagurney et al. (2007), Cruz and Wakolbinger (2008), Nagurney and Qiang (2009), Daniele (2010), and the references therein).

Moreover, it is now being increasingly recognized that seemingly disparate equilibrium problems, in a variety of disciplines, possess a network structure. Nevertheless, although deep connections and equivalences have been made (and continue to be discovered) between/among different systems through the network formalism, the majority of such systems, to-date, have been exclusively of a socio-technical-economic variety. For example, equivalences have been established between electric power generation and distribution networks and transportation network equilibrium problems as well as between transportation network equilibrium problems and financial networks with intermediation. Such connections enrich both theory and practice (cf. Nagurney et al. (2007) and Liu and Nagurney (2007)).

In this paper, we propose a dynamical systems model of predator-prey food networks and prove that its stationary points coincide with the set of equilibria through the corresponding variational inequality formulation. We consider multitiered predator-prey networks in which the top tier consists of primary prey and the bottom tier consists of the predators, whereas the middle tier acts as both prey and predator. For example, such ecological food webs may correspond to a fish ecosystem, where the top tier of network nodes would, in this case, consist of plankton populations, the middle tier of small pelagic populations, and the bottom

tier would be the marine predators.

The development of a dynamic model for predator-prey networks is important since it enables the tracking of dynamic trajectories over time and reinforces the importance of the equilibrium state. Here, we, for the first time, synthesize predator-prey networks with projected dynamical systems to construct a framework for the formulation, analysis, and computation of solutions to ecological food webs that captures the dynamic behavior and biology of predator-prey interactions.

This paper is organized as follows. In Section 2, we first extend the predator-prey model of Mullan, Shin, and Cury (2009) to capture both congestion as well as dynamics, with a focus on multi-tiered food webs consisting of primary prey, intermediate species, who can be both prey and predators, and primary predators. We then propose a dynamic adjustment process, whose set of stationary points coincides with the set of solutions to the variational inequality problem governing the predator-prey equilibrium conditions. In addition, we establish stability analysis results. We also specialize the model to two-tiered ecological food webs consisting of only prey and predator species.

In Section 3, we highlight the relationships between the ecological predator-prey network models and existing models in the literature but from different disciplines. In particular, we compare these models to both spatial price equilibrium models in regional science and economics, and to supply chain network equilibrium models in logistics, and establish equivalences. In Section 4, we propose an algorithmic scheme that iteratively tracks the evolution of biomass flows until an equilibrium is achieved and we provide convergence results. We also apply the algorithm to a fisheries application. In Section 5 we conclude with a summary and suggestions for future research.

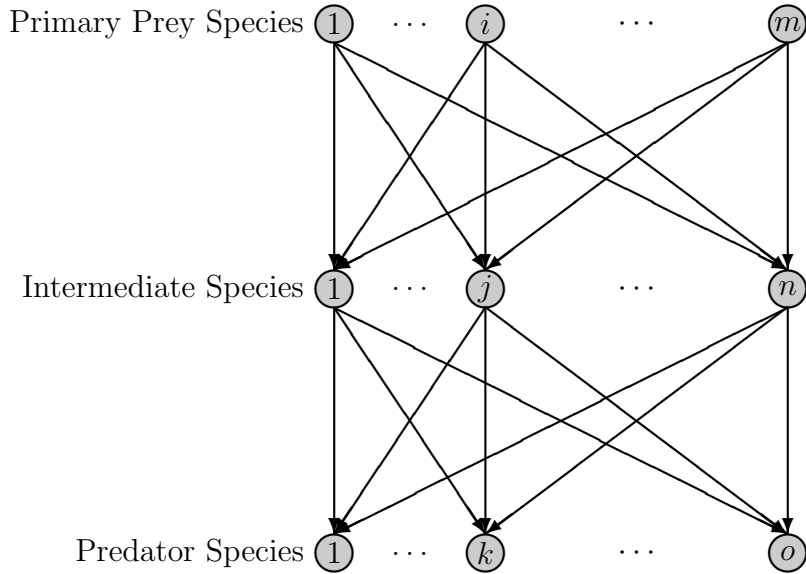


Figure 1: The Predator-Prey Ecosystem Network

2. The Dynamic Predator-Prey Network Model

In this Section, we develop the dynamic predator-prey network model, whose structure is given in Figure 1. Our work is inspired by the path-breaking paper of Mullon, Shin, and Cury (2009) which introduced variational inequality theory to this application domain by utilizing the novel network economics approach inspired by Nagurney (1999). We consider an ecosystem in which there are m distinct types of primary prey and o distinct types of predators with n intermediate species, which are both predators of the primary prey as well as prey of the predator species. Note that m , n , and o are, typically, distinct. The biomass of a species h is denoted by B_h . E_h denotes the inflow (energy and nutrients) of species h with the autotroph species, that is, the primary prey, in Figure 1, having positive values of E_h , whereas all predators have $E_h = 0$. The parameter γ_h denotes the trophic assimilation efficiency of species h and the parameter μ_h denotes the coefficient that relates biomass to somatic maintenance. The variable X_{hl} is the amount of biomass of species h preyed upon by species l and we are interested in determining their equilibrium values for all prey and predator species pairs (h, l) as well as the underlying dynamics of their interactions.

The prey equations that must hold for the top nodes in Figure 1 are:

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

Equation (1) states that, for each top-tiered 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, that must hold for the bottom nodes in Figure 1 are:

$$\gamma_k \sum_{j=1}^n X_{jk} = \mu_k B_k, \quad k = 1, \dots, o. \quad (2)$$

Equation (2) signifies that for each bottom-tiered predator species k , its assimilated biomass is equal to its somatic maintenance (which is represented by its coefficient μ_k times its biomass).

In addition, the following equation must hold for each intermediate species:

$$\gamma_j \sum_{i=1}^m X_{ij} - \sum_{k=1}^o X_{jk} = \mu_j B_j, \quad j = 1, \dots, n, \quad (3)$$

that is, the somatic maintenance of each such species is equal to its assimilated biomass minus the amount that it is preyed upon.

Equations (1), (2), and (3) are the conservation of flow equations, in network parlance, but from a biomass perspective.

In addition, there is a positive parameter $\hat{\phi}_{hl}$ for each prey/predator pair (h, l) that reflects the distance (note the spatial component) between distribution areas of prey h and predator l , with this parameter also capturing the transaction costs associated with handling and ingestion.

According to Mullon, Shin, and Cury (2009), the predation cost between each prey h and each predator l , denoted by F_{hl} , is given by:

$$F_{hl} = \hat{\phi}_{hl} - \kappa_h B_h + \lambda_l B_l, \quad (4a)$$

where $-\kappa_h B_h$ represents the easiness of predation due to the abundance of prey B_h and $\lambda_l B_l$ denotes the intra-specific competition of predator species l . We group the species biomasses and the biomass flows into the respective $m + n + o$ and $mn + no$ dimensional vectors B^* and X^* .

We now introduce the following extension. We assume that for each (h, l) there is now a function ϕ_{hl} that is a strictly increasing function of the biomass flow between h and l ; that is, we assume that

$$\phi_{hl} = \phi_{hl}(X_{hl}), \quad \forall h, l, \quad (4b)$$

where, for definiteness, we have that

$$\phi_{hl}(X_{hl}) = \eta_{hl} X_{hl} + \hat{\phi}_{hl}, \quad \forall h, l, \quad (4c)$$

where $\eta_{hl} > 0$, for all h, l . Such a function captures congestion. Consequently, the extended predation cost, \hat{F}_{hl} , that we utilize is given by:

$$\hat{F}_{hl} = \phi_{hl}(X_{hl}) - \kappa_h B_h + \lambda_l B_l, \quad \forall h, l. \quad (4d)$$

In view of (1), (2), (3), and (4d), we may write $\hat{F}_{hl} = \hat{F}_{hl}(X) \equiv F_{hl}(X, B)$, $\forall h, l$. Following then Mullon, Shin, and Cury (2009), we have the following definition of the governing predator-prey equilibrium conditions:

Definition 1: Predator-Prey Equilibrium Conditions

A biomass flow pattern $(X^*) \in R_+^{mn+no}$ is said to be in equilibrium if the following conditions hold for each pair of prey and predators (h, l) :

$$\hat{F}_{hl}(X) \begin{cases} = 0, & \text{if } X_{hl}^* > 0, \\ \geq 0, & \text{if } X_{hl}^* = 0. \end{cases} \quad (5)$$

The equilibrium conditions (5) reflect that, if there is a biomass flow from h to l , then there is an “economic” balance between the advantages ($\kappa_h B_h$) and the inconveniences of predation ($\phi_{hl} + \lambda_l B_l$), with the species biomasses B_h and B_l satisfying the corresponding equations (1) – (3) for every h and l .

Clearly, the predator-prey equilibrium conditions (5) may be formulated as a variational inequality problem, as given below.

Theorem 1

A biomass flow pattern $X^* \in R_+^{mn+no}$ is an equilibrium according to Definition 1 if and only if it satisfies the variational inequality problem: determine $X^* \in R_+^{mn+no}$ such that

$$\sum_{h,l} \hat{F}_{hl}(X^*) \times (X_{hl} - X_{hl}^*) \geq 0, \quad \forall X \in R_+^{mn+no}, \quad (6)$$

or, equivalently, the variational inequality: determine $X^* \in R_+^{mn+no}$ such that

$$\begin{aligned} & \sum_{i=1}^m \sum_{j=1}^n \left[\frac{\kappa_i}{\mu_i} \sum_{j=1}^n X_{ij}^* - \frac{\kappa_i \gamma_i}{\mu_i} E_i + \phi_{ij}(X_{ij}^*) + \lambda_j \left(\frac{\gamma_j \sum_{i=1}^m X_{ij}^* - \sum_{k=1}^o X_{jk}^*}{\mu_j} \right) \right] \times [X_{ij} - X_{ij}^*] \\ & + \sum_{j=1}^n \sum_{k=1}^o \left[\frac{\kappa_j}{\mu_j} \sum_{k=1}^o X_{jk}^* - \frac{\kappa_j \gamma_j}{\mu_j} \sum_{i=1}^m X_{ij}^* + \phi_{jk}(X_{jk}^*) + \frac{\lambda_k \gamma_k}{\mu_k} \sum_{j=1}^n X_{jk}^* \right] \times [X_{jk} - X_{jk}^*] \geq 0, \quad \forall X \in R_+^{mn+no}. \end{aligned} \quad (7)$$

Proof: Recall, as noted following (4d), that, for any predator-prey network, in view of equations (1) – (3), we may re-express B_h and B_l in terms of X and substitute the resultants into (4d) so that $\hat{F}_{hl} = \hat{F}_{hl}(X)$, $\forall h, l$. The equivalence between an equilibrium solution according to Definition 1 and variational inequality (6) then follows directly from using standard arguments as in Nagurney (1999) with the feasible set consisting solely of the nonnegative orthant since the constraints (1) – (3) have been embedded into the \hat{F}_{hl} for all h, l .

With notice to Figure 1, we obtain, specifically, using (1), (3), and (2), respectively:

$$B_i = \frac{\gamma_i E_i - \sum_{j=1}^n X_{ij}}{\mu_i}, \quad i = 1, \dots, m; \quad (8)$$

$$B_j = \frac{\gamma_j \sum_{i=1}^m X_{ij} - \sum_{k=1}^o X_{jk}}{\mu_j}, \quad j = 1, \dots, n, \quad (9)$$

and

$$B_k = \frac{\gamma_k \sum_{j=1}^n X_{jk}}{\mu_k}, \quad k = 1, \dots, o. \quad (10)$$

Hence, with the use of (4d) and (8) – (10), we have that

$$\hat{F}_{ij}(X) = \frac{\kappa_i}{\mu_i} \sum_{j=1}^n X_{ij} - \frac{\kappa_i \gamma_i}{\mu_i} E_i + \phi_{ij}(X_{ij}) + \lambda_j \left(\frac{\gamma_j \sum_{i=1}^m X_{ij} - \sum_{k=1}^o X_{jk}}{\mu_j} \right), \quad \forall i, j, \quad (11)$$

and

$$\hat{F}_{jk}(X) = \frac{\kappa_j}{\mu_j} \sum_{k=1}^o X_{jk} - \frac{\kappa_j \gamma_j}{\mu_j} \sum_{i=1}^m X_{ij} + \phi_{jk}(X_{jk}) + \frac{\lambda_k \gamma_k}{\mu_k} \sum_{j=1}^n X_{jk}, \quad \forall j, k, \quad (12)$$

and variational inequality (7) follows. \square

Remark

The above conservation of flow equations (1) – (3) hold, in fact, for any food web ecosystem of multiple tiers, and are not limited to the three-tiered network depicted in Figure 1. However, here, we focus on the ecosystem of the form in Figure 1 since we wish to relate predator-prey networks to existing supply chain network models as well as, in the bipartite case, to classical spatial price equilibrium problems.

We now present the dynamic model. In particular, due to the variational inequality formulation (6) (and (7)), we may exploit the connection between the set of solutions to a variational inequality problem and the set of solutions to a projected dynamical system

(cf. Dupuis and Nagurney (1993) and Nagurney and Zhang (1996a)). In so doing, a natural dynamic adjustment process becomes:

$$\dot{X}_{hl} = \max\{0, -\hat{F}_{hl}(X)\}, \quad \forall h, l. \quad (13)$$

According to (8), the rate of change of biomass flow between a prey and predator pair (h, l) is in proportion to the difference between the advantage of predation and the inconvenience, as long as the biomass flow, X_{hl} , between the pair is positive; that is, if $X_{hl} > 0$, then

$$\dot{X}_{hl} = -\hat{F}_{hl}(X). \quad (14)$$

However, since the biomass flows must be nonnegative, we must ensure that, when $X_{hl} = 0$, the flow does not become negative and, therefore, (8) must hold true.

Also, according to (13), if the advantage of preying on species h exceeds the inconvenience for predator l then the amount of biomass flow between h and l will increase; if, on the other hand, the inconvenience exceeds the advantage, then the biomass flow between this prey and predator pair will decrease. If the biomass flow between a pair is reduced to zero then it stays unchanged until the next positive signal, at which it increases at a rate given by (13).

The adjustment process in vector form for all prey and predator pairs is given by (15) below, where \hat{F} is the $mn + no$ -dimensional vector with components $\{F_{hl}\}$. Indeed, we can now write the following pertinent ordinary differential equation (ODE) for the adjustment process of biomass flows in vector form as (see also Nagurney and Zhang (1996a)):

$$\dot{X} = \Pi_K(X, -\hat{F}(X)), \quad (15)$$

where \hat{F} is the vector with components \hat{F}_{hl} ; $\forall h, l$, and

$$\Pi_K(X, v) = \lim_{\delta \rightarrow 0} \frac{(P_K(X + \delta v) - X)}{\delta}, \quad (16)$$

where

$$P_K(X) = \arg \min_{z \in K} \|X - z\|. \quad (17)$$

Note that, in the predator-prey network model, $K \equiv R_+^{mn+no}$.

A direct application of Theorem 2.4 in Nagurney and Zhang (1996a) yields the following result, since the feasible set K here is a convex polyhedron.

Theorem 2

X^* solves variational inequality (6)(equivalently, (7)), if and only if X^* is a stationary point of the ODE (15), that is,

$$0 = \Pi_K(X^*, \hat{F}(X^*)). \quad (18)$$

Theorem 2 establishes that the necessary and sufficient condition for a biomass flow pattern X^* to be in equilibrium in the predator-prey network is that X^* is a stationary point of the biomass flow adjustment process defined by ODE (15).

Note that for any $X_0 \in K$ as an initial value, we associate with ODE(\hat{F}, K) an initial value problem IVP(\hat{F}, K, X_0) defined as:

$$\dot{X} = \Pi_K(X, -\hat{F}(X)), \quad X(0) = X_0. \quad (19)$$

We now investigate stability properties of the above projected dynamical system (15). We first establish that $\hat{F}(X)$ is strictly monotone under the assumption that $\lambda_j = \kappa_j \gamma_j$; $j = 1, \dots, n$. We note that the ecologists Mullon, Shin, and Cury (2009) refer to this assumption as the strong equilibrium assumption.

Theorem 3

$\hat{F}(X)$ is strictly monotone, that is,

$$\sum_{h,l} [\hat{F}_{hl}(X^1) - \hat{F}_{hl}(X^2)] \times [X_{hl}^1 - X_{hl}^2] > 0, \quad \forall X^1, X^2 \in K, \quad X^1 \neq X^2. \quad (20)$$

Proof: Note that

$$\begin{aligned} \sum_{h,l} [\hat{F}_{hl}(X^1) - \hat{F}_{hl}(X^2)] \times [X_{hl}^1 - X_{hl}^2] &= \sum_{h,l} [F_{hl}(X^1, B^1) - F_{hl}(X^2, B^2)] \times [X_{hl}^1 - X_{hl}^2] \\ &= \sum_{i=1}^m \sum_{j=1}^n [\phi_{ij}(X_{ij}^1) - \phi_{ij}(X_{ij}^2)] \times [X_{ij}^1 - X_{ij}^2] \\ &\quad - \sum_{i=1}^m \kappa_i (B_i^1 - B_i^2) \times \left[\sum_{j=1}^n X_{ij}^1 - \sum_{j=1}^n X_{ij}^2 \right] \\ &\quad + \sum_{j=1}^n \lambda_j (B_j^1 - B_j^2) \times \left[\sum_{i=1}^m X_{ij}^1 - \sum_{i=1}^m X_{ij}^2 \right] \end{aligned}$$

$$\begin{aligned}
& + \sum_{j=1}^n \sum_{k=1}^o [\phi_{jk}(X_{jk}^1) - \phi_{jk}(X_{jk}^2)] \times [X_{jk}^1 - X_{jk}^2] \\
& + \sum_{j=1}^n -\kappa_j(B_j^1 - B_j^2) \times \left[\sum_{k=1}^o X_{jk}^1 - \sum_{k=1}^o X_{jk}^2 \right] \\
& + \sum_{k=1}^o \lambda_k(B_k^1 - B_k^2) \times \left[\sum_{j=1}^n X_{jk}^1 - \sum_{j=1}^n X_{jk}^2 \right]. \tag{21}
\end{aligned}$$

Using now equations (1), (2), and (3), the right-hand-side of equation (21) may be rewritten as:

$$\begin{aligned}
& \sum_{i=1}^m -\kappa_i(B_i^1 - B_i^2) \times [-\mu_i(B_i^1 - B_i^2)] \\
& + \sum_{j=1}^n \lambda_j(B_j^1 - B_j^2) \times \frac{\mu_j}{\gamma_j}(B_j^1 - B_j^2) + \sum_{j=1}^n \lambda_j(B_j^1 - B_j^2) \times \left(\frac{\sum_{k=1}^o X_{jk}^1 - \sum_{k=1}^o X_{jk}^2}{\gamma_j} \right) \\
& + \sum_{j=1}^n -\kappa_j(B_j^1 - B_j^2) \times \left[\sum_{k=1}^o X_{jk}^1 - \sum_{k=1}^o X_{jk}^2 \right] \\
& + \sum_{k=1}^o \lambda_k(B_k^1 - B_k^2) \times \frac{\mu_k}{\gamma_k}(B_k^1 - B_k^2) \\
& + \sum_{i=1}^m \sum_{j=1}^n [\phi_{ij}(X_{ij}^1) - \phi_{ij}(X_{ij}^2)] \times [X_{ij}^1 - X_{ij}^2] \\
& + \sum_{j=1}^n \sum_{k=1}^o [\phi_{jk}(X_{jk}^1) - \phi_{jk}(X_{jk}^2)] \times [X_{jk}^1 - X_{jk}^2]. \tag{22}
\end{aligned}$$

The first, second, and fifth summands in (22) are nonnegative whereas the sum of the third and fourth summands is equal to zero under the assumption that $\lambda_j = \kappa_j \gamma_j, \forall j$. Furthermore, due to (4c), we know that each of the last two summands in (22) is strictly greater than zero if $X^1 \neq X^2$. Hence, we have established that $\hat{F}(X)$ is strictly monotone. \square

We now state the following result.

Theorem 4

Since $\hat{F}(X)$ is strictly monotone, X^* is a strictly global monotone attractor, that is, there exists a $\delta > 0$ such that for all $X \in B(X^*, \delta)$:

$$d(X, t) = \|X \cdot t - X^*\| \tag{23}$$

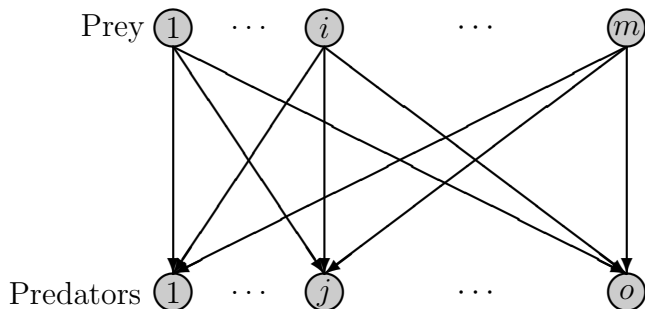


Figure 2: The Bipartite Network of an Ecosystem with Prey and Predators

is monotonically decreasing to zero in t for all $X \in K$, where $B(X, r)$ denotes the open ball with radius r and center X and $X \cdot t$ is the solution path of the initial value problem $IVP(\hat{F}, K, X)$ (19) that passes through X at time $t = 0$, that is, $X \cdot 0 = X(0) = X$.

Proof: Follows from Theorem 3.6 in Nagurney and Zhang (1996a). \square

Since we have established strict monotonicity of $\hat{F}(X)$ the following result is immediate from the fundamental theory of variational inequalities (cf. Nagurney (1999) and the references therein).

Theorem 5

The equilibrium X^ that satisfies variational inequality (6) is unique since $\hat{F}(X)$ is strictly monotone in X .*

It is important to emphasize that the projected dynamical systems model is non-classical since the right-hand-side in (10) is not continuous. A complete theory to handle such realistic dynamical systems which apply to systems in which there are constraints (as in numerous applications) has been developed by Dupuis and Nagurney (1993) and Nagurney and Zhang (1996) and the references therein. It is also worth emphasizing that there has been a long tradition in ecological modeling of dynamical systems, as in the classical work of Lotka-Volterra models (see also Odum (1971) and Scheffer and Carpenter (2003)). However, our work in this paper couples not only projected dynamical systems, which can handle constraints (such as nonnegativity of biomass flows), with network structure, but also economics and biology plus logistics.

It is worth mentioning that the above models collapse to a bipartite predator-prey network model (in static and dynamic forms, respectively), if there are no intermediary species. In this special case, the network is as depicted in Figure 2 and the variational inequality simplifies

to: determine $\hat{X}^* \in R_+^{mo}$, such that

$$\sum_{i=1}^m \sum_{k=1}^o \left[\frac{\kappa_i}{\mu_i} \sum_{k=1}^o X_{ik}^* - \frac{\kappa_i}{\mu_i} \gamma_i E_i + \phi_{ik}(X_{ik}^*) + \frac{\lambda_k \gamma_k}{\mu_k} \sum_{i=1}^m X_{ik}^* \right] \times [X_{ik} - X_{ik}^*] \geq 0, \quad \forall \hat{X} \in R_+^{mo}, \quad (24)$$

where $\hat{X} \equiv \{\{X_{ik}\} | i = 1, \dots, m; k = 1, \dots, o\}$.

3. Relationships to Spatial Price Equilibrium Problems and Supply Chain Network Equilibrium Problems

First, we establish the relationship between the bipartite predator-prey network model discussed in the preceding section and spatial price equilibrium problems, which have served as the foundation for a plethora of applications in regional science and economics (dating from the contributions of Samuelson (1952) and Takayama and Judge (1971)) from agriculture to energy and even finance (see, e.g., Labys and Yang (1997) and Nagurney (1999)).

If we define now

$$s_i \equiv \sum_{k=1}^m X_{ik}, \quad i = 1, \dots, m, \quad (25)$$

$$d_k \equiv \sum_{i=1}^m X_{ik}, \quad k = 1, \dots, o, \quad (26)$$

variational inequality (24) may be rewritten as: determine $(s^*, \hat{X}^*, d^*) \in K^1$, where $K^1 \equiv \{(s, \hat{X}, d) | \hat{X} \in R_+^{mo}, \text{ and (25) and (26) hold}\}$, such that

$$\sum_{i=1}^m \pi_i(s_i^*) \times (s_i - s_i^*) + \sum_{i=1}^m \sum_{k=1}^o \phi_{ik}(X_{ik}^*) \times (X_{ik} - X_{ik}^*) - \sum_{k=1}^o \rho_k(d_k^*) \times (d_k - d_k^*) \geq 0, \quad \forall (s, \hat{X}, d) \in K^1, \quad (27)$$

where

$$\pi_i(s_i) \equiv \frac{\kappa_i}{\mu_i} s_i - \frac{\kappa_i}{\mu_i} \gamma_i E_i, \quad i = 1, \dots, m, \quad (28)$$

$$\rho_k(d_k) \equiv \frac{-\lambda_k \gamma_k}{\mu_k} d_k, \quad k = 1, \dots, o. \quad (29)$$

Variational inequality (27) is precisely the variational inequality of the classical spatial price equilibrium conditions due to Samuelson (1952) and Takayama and Judge (1971), who, nevertheless, assumed that the unit transaction costs ϕ_{ik} were fixed, unlike the later work of Florian and Los (1982) and Dafermos and Nagurney (1984). The spatial price equilibrium conditions state that there will be a positive amount of commodity shipment between a pair of supply and demand markets if the supply price at the supply market plus the unit transportation cost is equal to the price at the demand market; if the former exceeds the latter

then the equilibrium commodity shipment between the pair of supply and demand markets will be equal to zero. Hence, expressions (25) and (26) correspond, respectively, to the “supplies” at the “supply markets,” and “demands” at the “demand markets,” whereas the functions (28) correspond to the “supply price” functions and the “demand price” functions, respectively, with the ϕ_{ik} playing the role of the unit transportation (or transaction cost). Nagurney, Takayama, and Zhang (1995) proposed projected dynamical systems models of spatial price network equilibria whereas Nagurney and Zhang (1996b) provided conditions for stability of solutions.

Recently, Nagurney and Nagurney (2011) explored the relationships between spatial price equilibrium problems and bipartite predator-prey networks but focused on models in which the unit transaction costs were fixed and not flow-dependent. In that case the underlying function that enters the variational inequality is monotone (and not strictly monotone). They also presented numerical examples.

We now identify the relationship, which is, in fact an equivalence, between the multitiered ecological predator-prey network equilibrium model and the supply chain network equilibrium model introduced in Nagurney, Dong, and Zhang (2002), which has formed the basis of numerous extensions (cf. Nagurney (2006) and the references therein). Recall that this model assumed that there are m competing, profit-maximizing manufacturers, n competing, profit-maximizing retailers, and consumers located at o demand markets. We first note that the model in Nagurney, Dong, and Zhang (2002) assumed that demand functions at the demand markets were given. We now, for definiteness, write down directly the governing variational inequality of supply chain network equilibrium (please refer to Nagurney, Dong, and Zhang (2002) for the basic model and to Nagurney et al. (2002) for the dynamic version). Our notation below follows that of Nagurney et al. (2002). In the Theorem below we have used the demand price functions rather than the demand functions, as in the original formulation, in order to make the connection to the predator-prey model more transparent.

Theorem 6 (Nagurney, Dong, and Zhang (2002))

A supply chain network equilibrium is equivalent to the solution of the variational inequality problem given by: determine the equilibrium vectors of product shipments, shadow prices, and retail shadow prices $(Q^{1}, Q^{2*}, \rho_2^*) \in K^2$, satisfying:*

$$\sum_{i=1}^m \sum_{j=1}^n \left[\frac{\partial f_i(Q^{1*})}{\partial q_{ij}} + \frac{\partial c_{ij}(q_{ij}^*)}{\partial q_{ij}} + \frac{\partial c_j(Q^{1*})}{\partial q_{ij}} - \rho_{2j}^* \right] \times [q_{ij} - q_{ij}^*] \\ + \sum_{j=1}^n \sum_{k=1}^o \left[\rho_{2j}^* + c_{jk}(Q^{2*}) - \rho_{3k}^*(d^*) \right] \times [q_{jk} - q_{jk}^*]$$

$$+ \sum_{j=1}^n \left[\sum_{i=1}^m q_{ij}^* - \sum_{k=1}^o q_{jk}^* \right] \times [\rho_{2j} - \rho_{2j}^*] \geq 0, \quad \forall (Q^1, Q^2, \rho_2) \in K^2, \quad (30)$$

where $K^2 \equiv R_+^{mn+no+n}$.

Note that, in order to connect the solution of variational inequality (30) with the solution of variational inequality (7), we make the identifications:

$$X_{ij} \equiv q_{ij}, \quad i = 1, \dots, m; j = 1, \dots, n, \quad (31)$$

$$X_{jk} \equiv q_{jk}, \quad j = 1, \dots, n; k = 1, \dots, o, \quad (32)$$

since biomass flows in the ecological network model correspond to commodity flows in the supply chain network equilibrium model. Also, the marginal transportation/transaction cost associated with pairs of manufacturers and retailers, denoted for (i, j) by $\frac{\partial c_{ij}(Q^{1*})}{\partial q_{ij}}$, corresponds to the cost ϕ_{ij} in the predator-prey model. Similarly, the unit transaction cost between a retailer and demand market pair (j, k) given by c_{jk} corresponds to ϕ_{jk} for each pair (j, k) , whereas the demand price function associated with a primary predator is then given by $\rho_{3k}(d) = \frac{-\lambda_k \gamma_k}{\mu_k} d_k$ for each k . Also, here we have that the marginal storage cost, denoted for a retailer j by $\frac{\partial c_j(Q^{1*})}{\partial q_{ij}}$, is precisely equal to zero for all j . The marginal production cost associated with a manufacturer i corresponds to $\frac{\kappa_i}{\mu_i} s_i - \frac{\kappa_i}{\mu_i} \gamma_i E_i$ in the ecological network model for each i .

The shadow prices ρ_{2j}^* in (30), in turn, correspond to: $\lambda_j \left(\frac{\gamma_j \sum_{i=1}^m X_{ij}^* - \sum_{k=1}^o X_{jk}^*}{\mu_j} \right)$ for each j and, fascinatingly, if $\gamma_j = 1$ for each j (which would mean that the trophic assimilation factor is equal to 1 for each intermediary species j), then ρ_{2j}^* is also precisely equal to: $\frac{\kappa_j}{\mu_j} \sum_{k=1}^o X_{jk}^* - \frac{\kappa_j \gamma_j}{\mu_j} \sum_{i=1}^m X_{ij}^*$ for each j (under the assumption of strong equilibrium, in which, as noted earlier, $\lambda_j = \kappa_j \gamma_j$ for each j). Moreover, since we expect that the intermediary species “clear” in economics terms, each of these prices would be positive and, therefore, the last term in variational inequality (30) before the greater than equal to sign would be equal to zero. Hence, we have established that ecological predator-prey networks act as nature’s supply chain networks by establishing the equivalence between the variational inequality governing supply chain network equilibrium given by (30) and the one governing ecological predator-prey network equilibrium given by (7)!

4. An Algorithm and Application

In this Section, we recall the Euler method which is induced by the general iterative scheme of Dupuis and Nagurney (1993), and which is designed to compute the stationary points of the projected dynamical system

$$\dot{X} = \Pi_K(X - \hat{F}(X)), \quad (33)$$

or, equivalently, according to Theorem 2, to determine solutions X^* to the variational inequality problem:

$$\langle \hat{F}(X^*)^T, X - X^* \rangle \geq 0, \quad \forall X \in K, \quad (34)$$

where $\langle \cdot, \cdot \rangle$ denotes the inner product in N -dimensional Euclidean space where here $N = mn + no$.

In particular, the Euler method takes, at iteration τ , the form:

$$X_{\tau+1} = P_K(X_\tau - a_\tau F(X_\tau)). \quad (35)$$

Here, for definiteness, we give the explicit formulae for (35) for the iterative computation of the biomass flows, which are made possible because of the simplicity of the underlying feasible set K .

In particular, with notice to (6) and (7), we have that:

$$X_{ij}^{\tau+1} = \max\left\{0, a_\tau \left(-\frac{\kappa_i}{\mu_i} \sum_{j=1}^n X_{ij} + \frac{\kappa_i \gamma_i}{\mu_i} E_i - \phi_{ij}(X_{ij}) - \lambda_j \left(\frac{\gamma_j \sum_{i=1}^m X_{ij} + \sum_{k=1}^o X_{jk}}{\mu_j}\right)\right)\right\}, \forall i, j, \quad (36)$$

and

$$X_{jk}^{\tau+1} = \max\left\{0, a_\tau \left(-\frac{\kappa_j}{\mu_j} \sum_{k=1}^o X_{jk} + \frac{\kappa_j \gamma_j}{\mu_j} \sum_{i=1}^m X_{ij} - \phi_{jk}(X_{jk}) - \frac{\lambda_k \gamma_k}{\mu_k} \sum_{j=1}^n X_{jk}\right)\right\}, \forall j, k. \quad (37)$$

The expressions (36) and (37) provide a discrete-time approximation to the dynamic trajectories associated with the continuous time evolution of the biomass flows according to (33) on the links of the ecological network depicted in Figure 1.

We now establish convergence of the Euler method applied to our model but first we need an assumption.

Assumption 1

Suppose that there exists a sufficiently large M , such that

$$F_{hl}(X) > 0 \tag{38}$$

for all predator-prey pairs (h, l) and all biomass flows X with $X_{hl} \geq M$.

Under Assumption 1, existence of an equilibrium X^* is guaranteed. We emphasize, however, that since $\hat{F}(X)$ is strictly monotone and linear, it is, hence, also strongly monotone, so existence of a solution to variational inequality (7) necessarily holds.

Theorem 7

Any sequence $\{X^\tau\}$ generated by the Euler method (35), with explicit realization for the solution of our model yielding expressions (36) and (37), with $a_\tau > 0$, for $\tau = 1, 2, \dots$, and

$$\lim_{\tau \rightarrow \infty} a_\tau = 0, \tag{39}$$

$$\sum_{\tau=1}^{\infty} a_\tau = \infty, \tag{40}$$

converges to a unique equilibrium point, satisfying (34) as well as (18).

Proof: Conditions (39) and (40) are required for convergence (see Assumption 4.1 in Nagurney and Zhang (1996a)). Setting the sequence $\{X^\tau\}$ is bounded, under Assumption 1, and $\hat{F}(X)$ is strictly monotone according to Theorem 4, and also $\hat{F}(X)$ is Lipschitz continuous since it is linear, all the conditions for convergence that are required are satisfied according to Theorem 4.1 in Nagurney and Zhang (1996a) (see also Theorem 6.10 therein). \square

The algorithm was considered to have converged to a solution when the absolute value of each of the successive biomass flow iterates differed by no more than $\epsilon = 10^{-5}$. We utilized (cf. (39) and (40)) the sequence $a_\tau = 1 \cdot \{1, \frac{1}{2}, \frac{1}{2}, \dots\}$, which satisfies the requirements for convergence of the Euler method. The computer system used was a Linux-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). Their data is for the coastal system of Chile and is based on previous papers of Neira and Arancibia (2004) and Neira, Arancibia, and Cubillo (2004). Here we report our complete input and output data for reproducibility purposes.

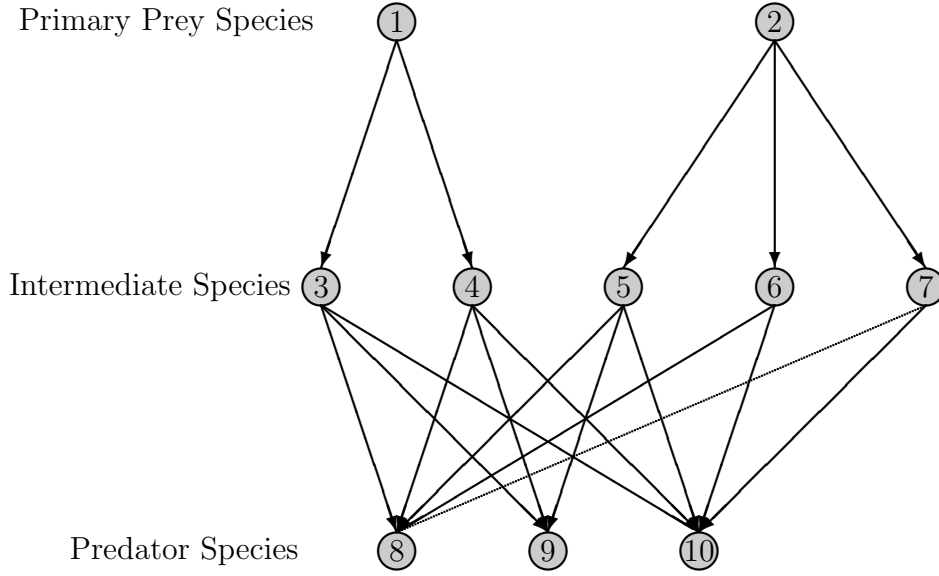


Figure 3: The Ecosystem for the Numerical Application

A Numerical Application

We now discuss an application that is drawn from fisheries and which is motivated by Mullon, Shin, and Cury (2009). The ecological predator-prey network is depicted in Figure 3. The species and their data parameters are itemized in Table 1, where note that fisheries as a predator is also included. There are 2 primary prey: the phytoplankton and the macrobenthos, 5 intermediate predator-prey species: the anchovies, the sardines, the pelagics I, the small hake, and the demersal fish I, and 3 bottom-tiered predators: the sea lions, the sea birds, and the fisheries.

The ϕ_{hl} functions (please refer to Figure 3 and (4c)) were given by:

$$\phi_{13}(X_{13}) = .08276X_{13} + 82.76, \quad \phi_{14}(X_{14}) = .08272X_{14} + 82.72,$$

$$\phi_{25}(X_{25}) = .00037X_{25} + .37, \quad \phi_{26}(X_{26}) = .00012X_{26} + .12, \quad \phi_{27}(X_{27}) = .00041X_{27} + .41,$$

$$\phi_{38}(X_{38}) = .00198X_{38} + 1.98, \quad \phi_{39}(X_{39}) = .00198X_{39} + 1.98, \quad \phi_{3,10}(X_{3,10}) = .00197X_{3,10} + 1.97,$$

$$\phi_{48}(X_{48}) = .00236X_{48} + 2.36, \quad \phi_{49}(X_{49}) = .00236X_{49} + 2.36, \quad \phi_{4,10}(X_{4,10}) = .00235X_{4,10} + 2.35,$$

$$\phi_{58}(X_{58}) = .00119X_{58} + 1.19, \quad \phi_{59}(X_{59}) = .00119X_{59} + 1.19, \quad \phi_{5,10}(X_{5,10}) = .00048X_{5,10} + .48,$$

$$\phi_{68}(X_{68}) = .0013X_{68} + 1.30, \quad \phi_{6,10}(X_{6,10}) = .00048X_{6,10} + .48,$$

$$\phi_{78}(X_{78}) = .00049X_{78} + .49, \quad \phi_{7,10}(X_{7,10}) = .00048X_{7,10} + .48.$$

The above functions are extensions of their uncongested counterparts extracted from Mullon, Shin, and Cury (2009).

Table 1: Species and Their Parameters

i	species	γ_i	μ_i	κ_i	λ_i	E_i
1	phytoplankton	2.00	16.89	.21	0.00	8000.00
2	macrobenthos	.25	.50	.23	0.00	25.00
3	anchovies	.1	.94	.26	.02	0.00
4	sardines	.10	1.10	.27	.02	0.00
5	pelagics I	.11	.13	.25	.02	0.00
6	small hake	.30	.56	.26	.08	0.00
7	demersal fish I	.20	.26	.23	.04	0.00
8	sea lions	.02	.15	0.00	.01	0.00
9	sea birds	.025	.50	0.00	.01	0.00
10	fisheries	.30	.08	0.00	.01	0.00

The equilibrium biomass flows computed by the Euler method were:

$$\begin{aligned}
 X_{13}^* &= 4658.79, & X_{14}^* &= 4665.89, \\
 X_{25}^* &= 0.00, & X_{26}^* &= 5.48, & X_{27}^* &= 0.00, \\
 X_{38}^* &= 142.13, & X_{39}^* &= 310.22, & X_{3,10}^* &= 5.10, \\
 X_{48}^* &= 141.53, & X_{49}^* &= 309.56, & X_{4,10}^* &= 4.46, \\
 X_{58}^* &= X_{59}^* = X_{5,10}^* = X_{68}^* = X_{6,10}^* = X_{78}^* = X_{7,10}^* &= 0.00,
 \end{aligned}$$

with the equilibrium species biomass levels being:

$$\begin{aligned}
 B_1^* &= 395.22, & B_2^* &= 1.54, & B_3^* &= 8.96, & B_4^* &= 10.03, & B_5^* &= 0.00, \\
 B_6^* &= 2.93, & B_7^* &= 0.00, & B_8^* &= 37.82, & B_9^* &= 30.99, & B_{10}^* &= 35.87.
 \end{aligned}$$

This application demonstrates that the dynamic ecological network framework developed in this paper can be utilized for the study of ecological predator-prey networks.

5. Summary and Conclusions

The contributions to the literature in this paper are:

- (1). a new dynamic ecological predator-prey network model, which captures the dynamics underlying multitiered ecological networks and that is based on an extension to capture congestion associated with predator-prey interactions, also developed here, of a model presented earlier by Mullan, Shin, and Cury (2009);
- (2). a proof that the set of stationary points of the projected dynamical systems model coincides with the set of solutions to the governing predator-prey equilibrium conditions, formulated as a variational inequality problem;
- (3). the establishment of existence and uniqueness results to the variational inequality problem plus stability results;
- (4). a proof of the equivalence between the governing equilibrium condition of the ecological predator-prey network and supply chain network equilibrium, as well as the proof that the special case of the bipartite network corresponds to the classical spatial price equilibrium problem;
- (5). a proof of the convergence for the proposed algorithm scheme, and
- (6) an applications to an ecological predator-prey network drawn from a fisheries application.

Our contributions in this paper further demonstrate the growing interconnections among network problems in different disciplines and also show that ecological food webs act and perform as nature's supply chains.

Future research is expected to include other applications of our framework to ecological networks.

Acknowledgments

The authors are grateful for the helpful comments and suggestions during the review of the original version of this paper.

Professor Anna Nagurney acknowledges helpful discussions with Dr. Christian Mullan regarding the data in his paper with Shin and Cury in 2009. She also acknowledges support from the John F. Smith Memorial Fund.

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