

**Ecological Transfers replace Economic Markets in
a General Equilibrium Ecosystem Model**

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Abstract

The oft-cited analogies between ecological and economic systems are exploited to develop a many-species model of population dynamics. In economies, markets are the fundamental institutions in which demand and supply determine the quantities and prices of goods. However, economic markets are not appropriate for ecological communities, because markets rely on voluntary exchange, whereas plants and animals engage in involuntary transfers of biomass. A properly defined counterpart to markets based on biomass transfers permits a general equilibrium model of predator/prey and competitive interactions in a many-species community. Functional response from optimal foraging and predation risk provide the demand and supply, respectively, in the biomass transfers. Energy per unit time is scarce and predators and prey make optimum choices with respect to functional response and risk avoidance based on required energy expenditures. The energy expenditures are similar to economic prices: they determine foraging strategies and are beyond the control of the predators and prey, yet they are determined by the aggregate choices of all predators and prey and by population densities. The energies acquired from foraging are used in a new way to construct difference equations that determine the population dynamics.

The earth's biological resource stocks yield flows of life-supporting benefits to human communities, yet there is growing evidence cited in popular and scientific publications about the decline of these resources (Peters, 1991; Perrings et al., 1995; Arrow et al., 1995; Grime, 1997; Daily, 1997; Barrett and Odum, 2000). The decline is driven by growing human consumption of the resources whose supplies are limited by biological carrying capacities. What and how much resources are consumed are determined largely by human choices manifested in economic market behavior, so an important step to understanding the decline is to understand the interplay between ecology and economics.

Perhaps the recognition of this interplay is responsible for the long history of analogies drawn between ecology and economics.¹ The idea that plants, animals and humans all face resource allocation problems under conditions of scarcity seems apparent, and economists and ecologists have borrowed from one another's fields to describe individual behavior under various environmental constraints.² For example, Stephens and Krebs (1986) and Robson (2001) compare optimum foraging theory with the theory of consumer behavior, and the analytical methods employed in both theories are closely related.

When analyses move from individual behavior to obtaining system-wide outcomes based on that behavior, the interconnectedness of the individuals is essential in both ecology and economics. However, the analogies between the two disciplines begin to dissipate because the desired outcomes diverge. Economists are interested in how market exchange in an economy determines the prices of goods that individuals take as signals of scarcity in their optimization

¹ A succession of analogies and influence can be traced from Adam Smith's *The Wealth of Nations* to Thomas Malthus' *An Essay on Principles of Population* to Charles Darwin's *The Origins of Species* and to Alfred Marshall's *Principles of Economics*.

² An incomplete list of contributors includes Penrose (1952), Rosen (1967), Hardin (1968), Rapport (1971), Tullock, (1971, 1999), Rapport and Turner (1977), Hirschleifer (1977), Amir (1979), Bloom, Chapin and Mooney (1985), Gutierrez (1996) and Ghiselin, (1999, 2000).

problems. Ecologists are interested in how population dynamics are determined by interactions among individuals and by the exchange of nutrients between abiotic and biotic parts of an ecosystem. In most of their work, economists are not interested in populations of individuals, and ecologists are not interested in an ecological equivalent of prices.

Along with divergent interests come divergent methodologies. Ecologists link populations and resources in sets of differential or difference equations that when solved determine equilibrium populations. Economists link markets together in general equilibrium (GE) models that determine the quantities of goods and their prices. The GE approach has been referred to as the most important development in economics in the twentieth century (Sandler, 2001).

By appealing to the oft-made analogies between economics and ecology, I show how these divergent methodologies can be integrated into a many-species, optimum foraging model that serves as a tool for understanding the organization of non-human communities. The model rejects economic market exchange as not appropriate for ecology; instead, a properly defined alternative to exchange based on transfers of biomass (and energy) between individuals is used. The transfer approach permits retention of GE modeling. Moreover, the foraging behaviors that give rise to the transfers are used to obtain difference equations for population dynamics. The ultimate goal is to integrate a GE ecological model with GE economic models to improve our understanding of the how economies and ecosystems interact, thus leading to policies that can reverse the decline of biological resources.

The paper proceeds by briefly outlining market exchange in economics and then pointing to its similarities and differences with ecology. Two fundamental differences between individual interactions in ecology and economics are identified, both of which follow from the observation

that demanders and suppliers engage in voluntary exchange in economic markets, but predators and prey engage in involuntary transfers in ecological communities (Rapport and Turner, 1977). The ecological transfer model is then introduced and general equilibrium defined, and the results of the equilibrium calculations are used to derive population adjustment equations.

Economic Markets

In economics, markets are institutions in which goods flow from suppliers to demanders and they are fundamental to economic analyses: every good is exchanged in a market and every market has a demand and supply side. Optimizing behavior by consumers and firms determines the individual demands and supplies, and for each good the individual demands and supplies are aggregated to the market level. The markets are linked in general equilibrium models to determine market-clearing prices that individual consumers and firms take as signals of scarcity in their optimization problems (Arrow, 1968; Ginsburgh and Keyzer 1997). The prices are the system-wide outcomes of aggregated individual behavior. Typically, economists do not investigate how the system-wide outcomes determine the populations of the individual consumers and firms.³ Changes in populations, if included at all, are usually represented by exogenous shocks.

Although firms and consumers are both demanders and suppliers, it will be convenient here to just think of firms buying and selling goods to one another. Collectively, all firms that sell a particular good are in an industry. I assume that each firm produces and sells only one type

³ Although human population is not treated as a variable in general equilibrium models, there is a substantial literature on human fertility (Becker (1960, 1965) provides early treatments.), and a relatively small literature on endogenous population and economy-wide outcomes (See Razin and Sadka (1995) for analysis and references). In addition, club theory explores the optimum number of people sharing a facility (Sandler and Tschirhart, 1997). Perhaps human population has not been at the forefront of economic analysis owing to its complexity. Human parents have children for a myriad of reasons, the two most studied being altruism and the provision of old-age security. The same motivations do not come into play in ecological models of population dynamics.

of output which makes an easier comparison to plants and animals that have but one type of biomass to supply. Industries are characterized by their structure (Tirole, 1989), and perfect competition is the structure that is most pertinent to ecology. Perfect competition is associated with industries such as agriculture wherein there are many firms (farmers) and no one firm can influence market outcomes, because, being just one of many firms, the amounts of goods it demands and supplies are very small compared to the industry amounts (Stiglitz, 1993). The implication is that each firm is a price taker: it has not control over the prices it pays for inputs or the price it charges for output. Nevertheless, the prices are endogenous to the system and determined by aggregate behavior.

Because demands and supplies are results of individual decision making, there must be some motivation that drives the decisions, otherwise the decisions will be inconsistent and studying them would be futile. For firms in an economy, the almost universally assumed motivation is profit maximization. The firm demands inputs from suppliers, transforms those inputs into an output via some production process, and then supplies the output to other firms. In the market, one firm's output is another firm's input, both of which are called that market's good. Other things equal, the higher the market-determined output price and the lower the market-determined input prices the greater is profit.

Consider a simple economic market for wheat composed of profit maximizing wheat firms and cereal firms. A representative wheat farmer maximizes profit given by:

$$\pi^w = p W^w - p^0 x^0 \quad (1)$$

where W^w is the amount of wheat the farmer chooses to grow, x^0 is the input, say fertilizer, used to produce the wheat (in reality there will be many inputs each sold in a separate market, and x^0 would be a vector of those inputs), and p and p^0 are the per unit prices of wheat and fertilizer,

respectively. The quantity of wheat produced depends on the quantity of fertilizer purchased according to the production function $W^w = f^w(x^0)$. The solution to the farmer's problem yields the farmer's wheat supply function given by:

$$W^w(p) \tag{2}$$

Assuming a well-behaved production function, it is easy to show that $\partial W^w / \partial p > 0$, or the supply of wheat curve is positively sloped. (Varian, 1992) (Not shown here and below is that W^w is also a function of p^0 .)

A representative cereal firm maximizes profit given by:

$$\pi^c = p^c C - p W^c \tag{3}$$

where W^c is the amount of wheat the firm chooses to buy, p^c and p are the per unit prices of cereal and wheat, respectively, and C is the quantity of cereal produced according to the production function $C = f^c(W^c)$. Note that p is an expenditure by the cereal firm and a receipt for the wheat farmer. The solution to the cereal firm's problem yields the cereal firm's wheat demand function given by:

$$W^c(p) \tag{4}$$

Again, assuming a well-behaved production function, it is easy to show that $\partial W^c / \partial p < 0$, or the demand curve is negatively sloped. (Varian, 1992) (W^c is also a function of p^c .)

Equilibrium price of wheat is determined in the wheat market where the sum of all cereal firms' demands must equal the sum of all wheat farmers' supplies. Assuming all farmers and firms are identical, then letting N^w and N^c be the number of farmers and firms, respectively, the market clearing condition is:

$$N^c W^c(p) = N^w W^w(p) \tag{5}$$

The wheat market is depicted in Figure 1. The demand curve labeled D represents the

left side of (5), or the aggregate demand over all cereal firms for wheat whose quantity is plotted on the horizontal axis. The supply curve labeled S represents the right side of (5), or the aggregate supply over all wheat firms. The price of wheat is plotted on the vertical axis. The quantity of wheat and the currency flow in opposite directions in the voluntary exchange. Where D and S cross is the market determined equilibrium price at which the total quantity demanded equals the total quantity supplied. The price is the signal of scarcity: it is what the cereal and wheat firms respond to when maximizing profit, and while no single firm can affect the price, it is determined through the actions of all firms. A market not in equilibrium is subject to market forces that move it toward equilibrium, although stability will depend on the slopes of the demand and supply curves. (Standard downward sloping demand curves and upward sloping supply curves exhibit stable equilibria (Silberberg, 1990).)

The demand and supply curves can be used to show some simple dynamics that occur in three vertically aligned industries. To do this, add to the wheat and cereal firms the fertilizer industry that sells fertilizer to firms in the wheat industry. Figure 2 illustrates the wheat and fertilizer markets where in the top panel D is the cereal industry's demand for wheat and S is the wheat industry's supply of wheat as in Figure 1, and in the bottom panel D is the wheat industry's demand for fertilizer and S is the fertilizer industry's supply of fertilizer. Points e in both panels are the initial equilibriums in which all firms in the three industries are maximizing their profits and the markets clear.

Next suppose that the number of wheat farmers decreases, perhaps because of consumer preferences shifting to more oats and fewer wheat products, or perhaps because a severe drought causes some wheat farmers to exit the industry. In the wheat market, the supply curve shifts

inward thereby increasing the market equilibrium price to cereal firms.⁴ The higher price of wheat lowers profits in the cereal industry, cereal firms exit, and the industry has fewer cereal firms. Simultaneously, in the fertilizer market, when the number of farms decreases the demand for fertilizer shifts inward and this drives down the equilibrium price. The lower price of fertilizer lowers profits in the fertilizer industry, fertilizer firms exit, and the industry has fewer fertilizer firms. The upshot is that if the number of wheat farmers decreases, both the number of cereal firms and fertilizer firms decrease too.

In practice, local, state and federal governments use GE models linking many markets, like those described above, from many industries to predict how quantities and prices will change following changes in tax policy, introduction of a new firms, or other exogenous shocks. GE models are an improvement over their forerunner input/output models whose linearity assumptions and fixed prices are very restrictive.

Similarities and Differences

A natural comparison between an economy and an ecosystem is to liken economic firms to individual plants or animals, and to liken economic industries to species (Hirschleifer, 1977; Bloom et al., 1985; Regev et al., 1998; Landa and Ghiselin 1999). This comparison is not universal, some authors have likened entire species to firms (Hannon, 1976; Crocker and Tschirhart, 1992). But this does not carry the analogy to the micro level, because in economics the decision maker is the firm, not the industry; therefore, to capture micro behavior in ecology, where individual plants and animals make decisions, the individual must be the firm and the

⁴ The supply curve is the sum of all individuals' supply curves; thus, fewer farmers means fewer supply curves to sum and the aggregate supply curve shifts inward. Following the shift, the market is in disequilibrium at the initial equilibrium price, because at that price demand exceeds supply. Thus, there is excess demand and some cereal firms want more wheat than they are getting at the initial equilibrium price. These firms bid up the price and the initial equilibrium moves up to the new intersection.

species the industry (Ghiselin, 1974). The structure of ecological industries is very appropriately perfectly competitive. In fact, the notion of perfect competition is probably more appropriate in ecology than in economics (Hannon, 1976): there are many individuals in the species and no one individual can influence the market outcomes, because the amounts of biomass it demands and supplies are small compared to the species amounts.

There is no single motivation for individual plants and animals that is as universally accepted as profit maximization is for firms. Some that are mentioned regularly are net energy maximization, foraging time minimization, or fitness maximization. Fitness is not easily quantified and many characteristics of individuals contribute to fitness so that it is necessary to establish functional relationships between the characteristics and fitness (Gray, 1987; Alexander, 1982). Some authors go further and claim that it becomes tautological nonsense to say fitness is maximized (Oster and Wilson, 1978). (Similar criticism has been leveled against the utility function in consumer economics.) Time as a maximand must be linked to something else such as minimizing time used to acquire a unit of energy in which case one can just as well use net energy per unit of time as done in optimum foraging models. Energy maximization has its roots with Lotka (1922), has been formalized in a manner similar to that used below (Hannon, 1971, 1976, 1979), and has been the most frequently chosen maximand (Herendeen).⁵ In addition, accumulating energy is usually assumed to contribute to fitness.

Given maximizing net energy per time unit as the motivation for the individual, I adopt the convention that for a plant its biomass is its demand, where it uses biomass to acquire energy through photosynthesis, and the biomass it loses to grazers is its supply. For an animal, the biomass it consumes and converts to energy is its demand, and biomass lost to predators is its

⁵ Some authors have examined objectives that apply to the entire system such as ascendancy (Ulanowicz, 1980) or exergy (Jorgensen, 1982, 1986).

supply. Of course, once an animal is successfully preyed upon, it is gone. No further maximization takes place for this individual. This discrete, zero/one problem can be resolved by assuming each animal represents the 'average' member of the species, and when the animal is captured it does not lose its entire biomass, but rather it loses biomass equal to the mean loss over all members of its species. Thus, plants and animals are assumed to be identical within a species, much the same as firms in a perfectly competitive industry are usually assumed to be identical.

Predators maximizing net energy intake per unit time is postulated in optimum foraging theory (Emlen, 1966; MacArthur and Pianka, 1966), and as stated in the introduction, optimum foraging theory is often compared to consumer theory in economics. However, comparing optimum foraging theory to the theory of firms selling their outputs to one another, instead of to consumer theory, is more consistent with likening individual plants and animals to firms, and species to industries as done here. Moreover, in consumer theory consumers are postulated to maximize their utility which is ordinal and non measurable. Firms, on the other hand, are postulated to maximize profits that are cardinal and measurable just as plants' and animals' net energies are cardinal and measurable. Consumers do not produce and supply goods, but firms do produce and are suppliers of goods just as plants and animals produce biomass that they supply to other animals.

Given the above similarities between economics and ecology, what are the differences? Demanders and suppliers engage in voluntary exchange in economic markets, but in ecology there is an involuntary transfer (Rapport and Turner, 1977). This observation accounts for two fundamental differences. First, in economic markets suppliers offer goods to demanders in exchange for a payment. In ecological markets prey offer biomass to predators in exchange for

nothing. The predators do pay a system-wide determined ‘price’ in terms of the energy used for searching, attacking and handling, but this energy price is lost to the atmosphere and does not benefit the prey. Second, in economic markets, the suppliers and demanders need each other for survival: without demanders the suppliers have no income, and without suppliers the demanders cannot produce. In ecology, predators need prey for survival, but the reverse does not hold.⁶ In fact, the prey may be better off without predators. But predators have no incoming energy without prey.

The first fundamental difference can be seen by trying to translate Figure 1 into ecology. Let the demanders (cereal firms) be members of a predator species and the suppliers (wheat firms) be members of a prey species. The quantity on the horizontal axis now is the biomass of the prey species. As in the economic market, the predator species’ demand can be interpreted as the aggregate of all individual predators’ demands, where the demands are derived from the predators’ net energy maximization (or optimum foraging) problems that are detailed below. That is, a predator must spend energy to acquire biomass and the predator observes the different energy prices it must spend to attack and handle different prey. (This is analogous to a firm observing the different monetary prices, or scarcity signals, it must pay to obtain inputs.) The predator maximizes net energy flow by choosing a combination of prey biomasses such that the ratios of energy gained to energy price across all prey are equal according to the marginal value theorem. (Charnov, 1976) Again, details of this maximization process are given below. Therefore, the predator’s demand depends on the energy price, and for any one biomass type the energy price is on the vertical axis as in Figure 1.

However, unlike in the economic market where the supplier receives the price paid by the

⁶ Prey populations may exhibit more instability in the absence of predators, but the absence is unlikely to threaten prey survival. Predator survival, however, is impossible without prey.

demanders, the prey does not receive the energy price paid by the predator. Captured prey does lose biomass to the predator, who converts it to energy, but this energy is what is transferred, it is not the price. In fact, if energy is thought of as currency, then unlike economic models of exchange where the good flows from the supplier to the demander and currency flows in the opposite direction, in ecological transfer both the biomass and currency flow in the same direction. The prey does lose energy to the atmosphere if it attempts to escape, but this energy also does not flow to the predator. The point is that if we do not deviate from the economic analogy, then the prey does not take as a signal the energy price that the predator takes as a signal, and the energy price does not enter the prey's net energy maximization problem. Therefore, there is no supply curve as a function of the energy price as shown in Figure 1. Without a supply curve the analogy between ecological transfers and economic markets is problematic.⁷ Below I show how this problem can be overcome by using escape energy to develop the ecological counterpart to a supply curve.

The ramifications of the second fundamental difference between economic and ecological markets are apparent once we move to food webs and dynamic adjustments. Suppose an herbivore species replaces the fertilizer industry, a predator species replaces the wheat industry, and a top predator species replaces the cereal industry. The dynamics of the economic markets held that from equilibrium if the number of wheat firms decreases, then the numbers of fertilizer and cereal firms also decrease. But in the food chain, if the number of predators decreases, perhaps after being harvested by humans, then the number of top predators likely decreases, but the number of herbivores likely *increases*. Because the dynamics in the three-industry economic

⁷ Gutierrez (1996) develops interesting models in terms of demand and supply. The models differ in several important ways with standard economic demand and supply and the ecological model herein. Most importantly, his individual plants and animals are not optimizing subject to constraints. Instead demand and supply are subject to fixed maximum and minimum rates. Also, there is no analog to energy prices that are signals of scarcity to the individual and determined by the aggregate behavior of all individuals.

example follow from any market in which demands are negatively sloped and supplies are is positively sloped, the multi-market dynamics that follow from economic markets are wrong for ecological transfers. In the ecological transfer model this discrepancy is resolved.

Defining Ecological Transfers

An ecosystem transfer between predator and prey species, that is defined here as the analog to a market exchange in economics, is a variant of optimum foraging models.⁸ The latter models specify times for locating, attacking and handling prey that vary over species and sum to total time allocated to foraging. In the transfer model, time is not broken down, but rather a total time is specified, which we assume to be a reproductive cycle, and the predator chooses quantities of prey biomass over this time in response to the energy that must be spent to obtain the prey.

Starting with the predator and its demand, a representative predator is assumed to forage as if to maximize net energy given by:

$$R^d = [e^y - e]x^d - r^d(x^d) - \beta^d \quad (6)$$

where the e terms are in energy units per biomass units (e.g., kcalories/kilograms (kcal/kg)) and the x is biomass flows (e.g., kgs/year (kg/unit time)). R^d is in power units (e.g., Watts). The predator chooses the biomass flow, x^d , that is its demand, and for each unit of biomass there are e^y units of energy where e^y is the energy content in a unit of prey biomass. The e is the energy price paid to locate, attack and handle a unit of prey biomass, and it is to be determined in the ecological transfer. The function r^d is respiration or energy lost to the atmosphere that depends on biomass consumed and includes feces, locomotion, and reproduction, and β^d is resting metabolic

⁸ The proposed model is confined to predator/prey and competitive relationships; mutualism and other types of relationships are not considered.

rate that is independent of x^d . The solution to the predator's problem yields the predator's demand function given by:

$$x^d(e) \tag{7}$$

Assuming a well-behaved respiration function, it is easy to show that $\partial x^d/\partial e < 0$, or the predator's demand curve is negatively sloped.⁹

To develop the supply side of the ecological transfer, consider a representative member of the prey species that is assumed to maximize net energy given by:

$$R^y = [e^0 - e^p]x^y - r^y(x^y) - \beta^y - e^y[1 + t(e)]g(x^y) \tag{8}$$

The first three terms on the right side of (8) carry the same meaning as for the predator in (6), except the prey is obtaining biomass and energy from whatever species it preys on. (If this is a plant, predation is on the sun and e^0 is the energy photosynthesized per unit of plant biomass.)

The third term provides the supply side. The function $g(x^y)$ is the quantity of biomass supplied by each prey individual to the predators, and e^y is the energy embodied in a unit of prey biomass that also appears in the predator's income term in (6). In maximizing (8), the prey would prefer to supply zero biomass to the predator because outflows reduce net energy. However, the prey can supply zero biomass only if it demands zero biomass from its own prey in the sense that to attack its own prey, the prey risks being attacked by predators. Moreover, the more the prey feeds on its prey, the more it is exposed and the more biomass it supplies to predators. This predation risk is responsible for providing the supply side in the ecosystem market. The analogy to the economic market is that the cereal manufacturer would rather not have to spend money on buying wheat since this lowers profit, but if it did not buy wheat, it could not produce cereal.

⁹ Given $R^d = [e^y - e]x^d - r^d(x^d) - \beta^d$, the first-order condition for a maximum is $F(x^d, e) \equiv \partial R^d/\partial x^d = e^y - e - \partial r^d(x^d)/\partial x^d = 0$ and the sufficient second order condition is $\partial F(x^d, e)/\partial x^d = \partial^2 R^d/\partial x^{d2} = -\partial^2 r^d(x^d)/\partial x^{d2} < 0$. Using the implicit function theorem, the slope of the demand curve is $\partial x^d/\partial e = -(\partial F(x^d, e)/\partial e)/(\partial F(x^d, e)/\partial x^d) = -(-1)/\partial^2 r^d(x^d)/\partial x^{d2} < 0$.

Therefore, the cereal firm voluntarily buys wheat to produce and sell cereal. Similarly, the prey “voluntarily” exposes itself to the predator in order to feed.

The term t in (8) can be thought of as a tax on the prey, and it is important for deriving a supply curve. The representative prey loses energy to the predator when it is attacked and captured equal to $e^y g(x^y)$. Also, regardless of whether or not it is attacked, the prey loses energy to the atmosphere by avoiding or attempting to avoid attack. This latter energy (e.g.s, physical defense and allelopathy) is represented by t . If the avoidance energy is related to the energy that the predator spends to search for, attack and handle the prey, then we can justify writing $t = t(e)$ so that the tax is a function of e . Moreover, if greater predator energy expenditures on locating and attacking prey implies greater energy expenditures by the prey in avoidance, then, assuming differentiability, $dt(e)/dt > 0$. Using this tax, the solution to the prey’s problem yields the prey’s supply function given by:

$$g(x^y(e)) \tag{9}$$

Because $dt(e)/dt > 0$ and assuming a well-behaved respiration function, it is easy to show that $\partial g(x^y)/\partial e < 0$, or the prey’s supply curve is negatively sloped. (See footnote 7.)

The predators are engaging in exploitative competition for the prey, and this competition is manifested in the energy price paid by predators for prey. The equilibrium value for the energy price is a system-wide indicator of scarcity much the same as price is in an economic market. The energy price is determined in the ecological transfer where the sum of all predators’ demands equals the sum of all preys’ supplies. Assuming all predators and prey in a species are identical, then letting N^d and N^y be the density of predators and prey, respectively, the ecological transfer clearing condition is:

$$N^d x^d(e) = N^y g(x^y(e)) \tag{10}$$

Figure 3 illustrates three species in two transfers with negative sloped supply curves. If we assume that positive (negative) net energy increases (decreases) fitness and, therefore, increases (decreases) density, then the following dynamics follow. (The link between net energy and density is shown in the next section.) In the top panel, D is the top predators' aggregate demand for predator biomass and S is the aggregate supply of predator biomass. In the bottom panel, D is the predators' aggregate demand for herbivore biomass and S is the aggregate supply of herbivore biomass. Suppose the density of predators is decreased through human harvesting. In the top panel the predator supply curve shifts inward thereby raising the equilibrium price to the top predators from e to e' .¹⁰ A higher price lowers top predator net energy and their density decreases. Simultaneously, in the herbivore biomass market, when the predator is harvested the demand for herbivores shifts inward and this drives down the equilibrium energy price. The lower price predators pay to obtain herbivores also lowers the energy tax herbivores pay to avoid attack by predators, implying that herbivores are willing to accept more predation risk, increase their own biomass demands and increase their net energy. Consequently, their density increases. The negatively sloped supply curve, although rare at best in economics, is reasonable in ecology and is a way to account for standard population movements.

I have assumed the supply curve slope is steeper than the demand curve as depicted in Figure 3. Such a configuration exhibits Walrasian stability in economic markets. If the slopes are negative but their steepness reversed, the market is said to exhibit Marshallian stability. In the ecological transfer of Figure 3, reversing the steepness would imply that decreases in the predator population decreases the herbivore population. If the supply curve is vertical, there would be no population movements following energy price changes. Because the demand and

¹⁰ The supply curve is the sum of individuals' supply curves; thus, after harvest there are fewer individual curves to sum and the aggregate supply curve shifts inward.

supply curve slopes are derived from predation risk and energy lost in avoiding predation, testable hypotheses linking risk and energy losses to population changes can be formulated.

Before developing the link between net energy maximization and population updating, comparing traditional optimum foraging theory to the maximizing behavior of a predator with an objective function like those in (6) and (8) may be useful. To do this, add a second prey for a predator that is also preyed upon so that its objective function is:

$$R^d = [e^{y^1} - e^1]x^{d1} + [e^{y^2} - e^2]x^{d2} - r^d(x^{d1}, x^{d2}) - \beta^d - e^d[1 + t(e)]g(x^{d1}, x^{d2}) \quad (11)$$

where the numerical superscripts now refer to two different prey. Note that the predator's objective function given by (11) contains no prey population densities. The predator is not omniscient in that it does not require information on prey abundances. Instead, the predator responds to the difference between the energy content of the prey and the energy price it must expend. The energy prices are determined by prey and predator populations (via (10)), but these prices are system-wide determined values. This formulation may be more behaviorally plausible than the functional response representation of the individual in optimal foraging theory, because the predator is less likely to conduct inventories of prey species than it is to compare energies it loses to capture different prey.

In maximizing (11) over x^{d1} and x^{d2} , the Kuhn-Tucker optimality conditions with respect to the i^{th} , $i = 1, 2$, prey are:

$$\begin{aligned} \partial R^d / \partial x^{di} &= e^{y^i} - e^i - \partial r^d(x^{d1}, x^{d2}) / \partial x^{di} - e^d[1 + t(e)] \partial g / \partial x^{di} \leq 0 \\ x^{di} \partial R^d / \partial x^{di} &= 0 \quad \text{and} \quad x^{di} \geq 0 \end{aligned} \quad (12)$$

Together, these three conditions imply that if the predator consumes the i^{th} prey so that $x^{di} > 0$, then the marginal energy gained per biomass unit consumed (e^{y^i}) equals the sum of marginal energy losses to locating, attacking and handling (e^i), to respiration ($\partial r^d(x^{d1}, x^{d2}) / \partial x^{di}$), and to

predation and escaping ($e^d[1 + t(e)] \partial g / \partial x^{di}$). Alternatively, if the marginal energy gained is less than the sum of the energy losses, the i^{th} prey is not consumed. In this way prey are “ranked” according to their profitability as in optimum foraging theory, and a prey that does not provide the predator with at least as much energy as it costs to attack and handle is avoided (Stephens and Krebs, 1986; Robson, 2001).

If both prey types are consumed, then the marginal gain/marginal loss ratios are equal across the prey species:

$$\frac{e^{y1}}{e^1 + \partial r^d / \partial x^{d1} + e^d[1 + t(e)] \partial g / \partial x^{d1}} = \frac{e^{y2}}{e^2 + \partial r^d / \partial x^{d2} + e^d[1 + t(e)] \partial g / \partial x^{d2}} \quad (13)$$

Because the ratios in (13) depend on the transfer-determined energy prices, their magnitudes may change with changing transfer conditions in which case the predator exhibits switching behavior. By continuity of the objective functions, switching will be gradual over a range of energy prices, although when the ratio of prices, e^{y1} / e^{y2} , becomes large (small) enough the predator will specialize in only prey two (one). Furthermore, because optimization of (11) is done for a given set of population densities, and these densities change period to period as described below, the relationship between the demands, or the optimum x^{di} , and the densities are the predator’s functional responses. Instead of the rarely observed stepwise changes in functional response predicted by optimal foraging theory, the transfer model’s gradual switching is more realistic (van Baalen et al., 2001).

The predictions of the optimization model used here are similar to predictions of other optimum foraging models; for example, the models predict that prey are “ranked” according to their profitability, and a prey that does not provide the predator with at least as much energy as it costs to attack and handle is avoided (Stephens and Krebs, 1986; Robson, 2001). However,

extensive comparisons of the models are possible only if the time scales are the same. Unlike other foraging models, there is no distinction here between sequential versus simultaneous prey encounters, nor is time broken down into searching, attacking and handling times; therefore, the model is not useful for predicting predator activity over relatively short hunting periods. (Similarly, in economic models consumer demands are usually calculated over a month or a year as opposed to demands over a daily shopping spree.)

However, the activities modeled here take place in some time period, and as discussed in the next section the time period is assumed to be a reproductive cycle that exceeds a hunting period and can be many months depending on the species. During each reproductive cycle the transfer energy prices are determined and the individuals optimize given those prices. This process is termed a short-run equilibrium below, and the equilibrium results yield the individuals' net energies that in turn determine population changes as described below. After the populations change, the next time period starts. The model here is useful for studying community structure over time because it can account for many species in predator/prey relationships simultaneously, and allow for the individuals in the species to exhibit energy efficient foraging by responding to system-wide signals that are determined by that foraging. The model also exhibits energy balance because the total incoming energy to plants equals the total net energy acquired by all plants and animals plus the total energy lost to the atmosphere via respiration, metabolism, escaping predators, and searching for, attacking and handling prey (Tschirhart, 2000).

From the Individual to the Population

A short-run community transfer equilibrium is said to be attained when all individuals in all species are maximizing their net energies given the energy prices they face, and demand equals supply in every transfer at these prices. The equilibrium is determined by solving a system of equations for each biomass demand (the x 's in (6) and (8)), and for each energy price. There is an equation similar to (10) for each transfer to determine that transfer's energy price, there is one equation for the plant transfer where plants "prey" on the sun (Tschirhart, 2000, 2002), and there is one equation for each predator-prey transfer among the animals or for animals grazing on plants. These latter equations are the first-order conditions from the predator net energy maximization problems. The short-run community transfer equilibrium is attained over a period of time in which the all populations are constant. However, populations change in the long run according to the success of the individuals in acquiring net energy. As shown below, if individuals in a species have positive (zero, negative) net energy in a short-run equilibrium this period, then next period their population will increase (remain the same, decrease).¹¹ In long-run equilibrium, all individuals have zero net energy.

A community in short-run equilibrium moves toward long-run equilibrium or a steady state through adjustment in the populations that will move the species toward zero net energy. (Tschirhart, 2000; Pethig and Tschirhart, 2002) The transfer forces set in motion work as follows. Suppose predators in a species have positive net energy in the short run so their population increases. This increase lowers the energy price top predators must pay to attack the predators, because the predators are more plentiful. Top predators' demands for the predators increase (as per $\partial x^d / \partial e < 0$ from above), the predators supplies to the top predators increase,

¹¹ The economic analogy in a general equilibrium model is that if firms in an industry enjoy positive (zero, negative) profit in the short run, then in the long run the number of firms will increase (remain the same, decrease). Similar dynamics are discussed by Gutierrez (1996) where he relates positive (negative) assimilation rates with positive (negative) growth.

and predators' net energies decrease. In addition, the energy price paid by predators for their prey increases as there is more intra-species competition when the predator population grows. This price movement will also reduce the predator net energy as they demand less prey (Footnote 7). For a species with negative net energy in short-run equilibrium, the energy prices move in the opposite directions, and again the species moves toward zero net energy.

Discrete population update equations follow from the individuals' objective functions. First, consider a top predator. In steady-state it must be the case that births equals deaths in each time period, and if s is the lifespan of the representative individual, then the total number of births and deaths must be N/s . Dividing the totals by N yields the per capita steady-state birth and death rates:

$$1/s \tag{14}$$

The top predator's maximized net energy is given by $R^d(x^d(\mathbf{N}), e(\mathbf{N})) = R^d(\cdot)$ which is obtained by substituting the top predator's demands and energy prices, as functions of the populations, into its net energy objective function. \mathbf{N} is a vector of all species' populations and the demands and prices are the solutions to the short-run community transfer equilibrium wherein populations are fixed. In the steady state, $R^d(\cdot) = 0$. Reproduction requires energy and, by the definitions of the terms in (6), that energy is contained in the variable respiration. Let r^{ss} be the steady-state variable respiration, and let ρr^{ss} be the proportion of this variable respiration devoted to reproduction. Thus, in steady state the energy given by ρr^{ss} yields a per capita birth rate of $1/s$. Next, suppose the top predator is not in steady state and that $R^d(\cdot) \neq 0$ and variable respiration is r . Assuming that the proportion of $R^d(\cdot)$ that is available for reproduction is the same as the proportion of variable respiration available for reproduction, the energy now available for reproduction is $\rho [R^d(\cdot) + r]$. Finally, assuming that reproduction is linear in

available energy, then it follows that if ρr^{ss} yields a per capita birth rate $1/s$, then $\rho [R^d(\cdot) + r]$ yields a per capita birth rate of:

$$(1/s)[R^d(\cdot) + r] / r^{ss}. \quad (15)$$

The change in population is obtained by multiplying the population by the difference between the birth and death rates, where I assume the latter rate is independent of energy available for reproduction. Therefore, using (15), the population adjustment equation is

$$\begin{aligned} N^{t+1} &= N^t + N^t \left[\frac{1}{s} \frac{R^d(\cdot) + r}{r^{ss}} - \frac{1}{s} \right] \\ &= N^t + N^t \frac{1}{s} \left[\frac{R(\cdot) + r}{r^{ss}} - 1 \right] \end{aligned} \quad (16)$$

Expression (16) reduces to the steady state if $R^d(\cdot) = 0$ (in which case $r = r^{ss}$), because the bracketed term is zero. Alternatively, $R^d(\cdot) > (<) 0$ implies that $r > (<) r^{ss}$, in which case population increases (decreases).

If the species is not a top predator and is prey for another species, then in steady state the births must equal the deaths *plus* any individuals lost to predation. With predation, the death rate is $d = (1 - P(s))/s$ where $P(s)$ is the predation in each period for an individual that lives s periods. This predation can be written:

$$1 - P(s) = 1 - p - p(1-p) - p(1-p)^2 - p(1-p)^3 - \dots - p(1-p)^{s-1} \quad (17)$$

where each period p is the percentage of the prey taken from what is remaining of the prey from previous periods. Therefore, summing (17), the death rate is $d = (1-p)^s/s$. In steady state, the birth rate equals the death rate plus the predation rate, so the birth rate is $d + p$ or

$$p + (1-p)^s/s \quad (18)$$

Using (18) instead of (14) as the steady-state birth rate in deriving (16), the population update equation becomes

$$N^{t+1} = N^t + N^t \left[p + \frac{(1-p)^s}{s} \right] \left[\frac{R(\cdot) + r}{r^{ss}} - 1 \right] \quad (19)$$

When the representative prey solves (8) or (11) for x^y and x is substituted into g , $g(x^y)$ is the optimum amount of biomass supplied by a representative individual prey in each period.

Therefore, $p = g(x^y)/w$ is the predation rate on this prey where w is the prey weight so that p is in percent of an individual.

Update equation (19) shows that population changes are linked to foraging behavior through the individuals' objective functions. Moreover, in non steady state, the terms in (19) (i.e., $R(\cdot)$, r and p) will change period to period depending on the transfer interactions of all species.

Conclusion

The proposed transfer-based ecological model is in two stages. First, given species' populations, individual net energy maximization yields biomass demands and supplies that are aggregated to determine a short-run transfer equilibrium. The equilibrium yields the energy prices, or the system-wide signals that the individuals respond to when maximizing. Second, the maximum net energies attained in the short-run equilibrium are used to update the populations. If the two steps are repeated until there are no further population changes, which is reasonable because transfer sets in motion forces that move populations to zero net energy, then a steady state is reached. In practice, the general equilibrium model can be simulated with large numbers of species; therefore, the simultaneous functional responses of a predator consuming multiple prey can be easily tracked.

Finnoff and Tschirhart (2002a, 2002b) develop an earlier version of a transfer-based, general equilibrium ecological model for a marine ecosystem in the eastern Bering Sea and then

allow for human intervention. The system consists of eight species, including mammals, fish and plankton, and humans are introduced through the walleye pollock (*Theragra chalcogramma*) fishery, one of the world's largest. The model tracks how changes in human harvesting affect the populations of the eight species, and how these population changes affect future harvest decisions. Steller sea lions (*Eumetopias jubatus*), an endangered species, are one of the mammals, and the model indicates that commercial pollock fishing accounts for 16% of the sea lions' decline. Killer whales (*Orcinus orca*) are another one of the mammals and greater fishing quotas and fewer sea lions also means fewer killer whales and a negative impact on the whale watching industry. Data for the transfer model of the Alaskan ecosystem were taken from existing literature and include species population estimates, plant and animal biomasses, animal biomass demands, energy embodied in plant and animal biomass and resting metabolic rates. Because the transfer-based model is relatively easily integrated with standard economic models, it is useful for understanding the interdependencies between economies and ecosystems.

The transfer model omits the rich detail and behavior such as mutualism or social cooperation found in the Bering Sea and other real communities. By assuming all individuals in a species are identical the work does not contribute to the literature on individual-based models wherein species comprise heterogeneous individuals (DeAngelis and Gross, 1992). The model cannot explain, for example, how in a forest of even-aged monospecific stands, slight differences in initial resource allocations can lead to some trees outgrowing others. Two useful extensions of the model would be to introduce age distributed populations and abiotic factors such as temperature.

The shortcomings of the transfer-based general equilibrium model apply equally well to economic general equilibrium models. In the latter there is no detail on the physical traits,

personalities or family structures of consumers, nor the locations, working environments or hierarchal structure of the firms. The consumers and firms are represented solely by their market demands and supplies. Nevertheless, economic market-based models have proven to be very useful in shaping public policy, and perhaps the transfer approach can be similarly useful.

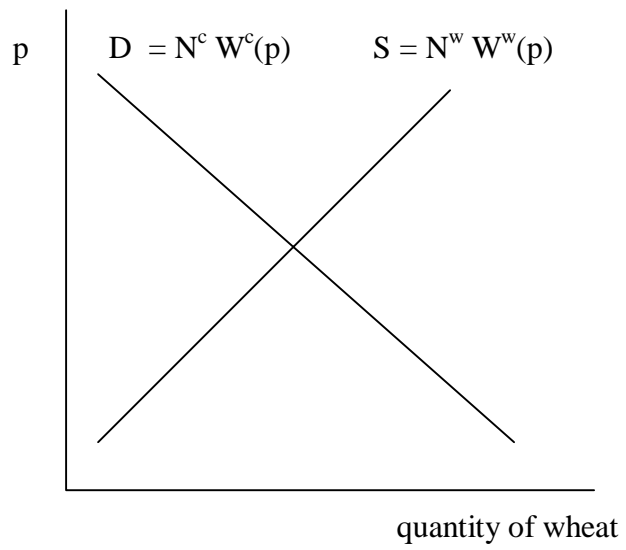


Figure 1 – Wheat market

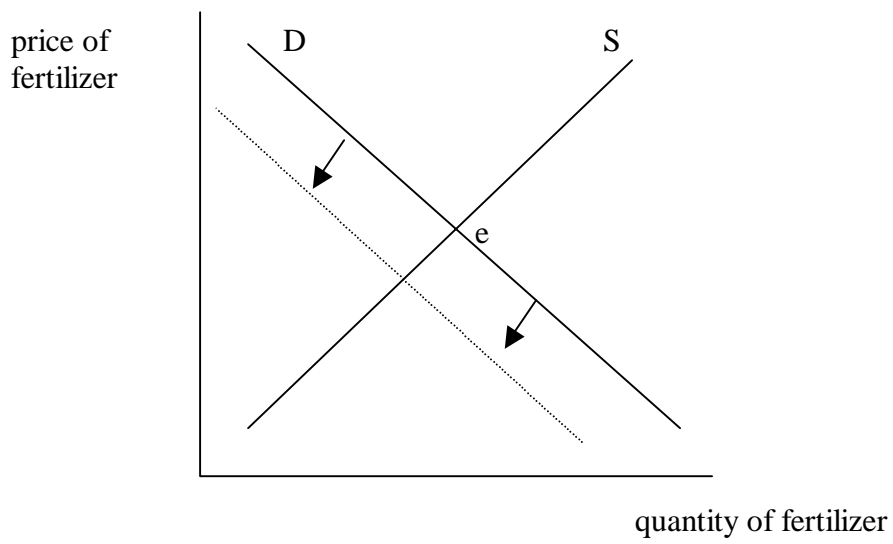
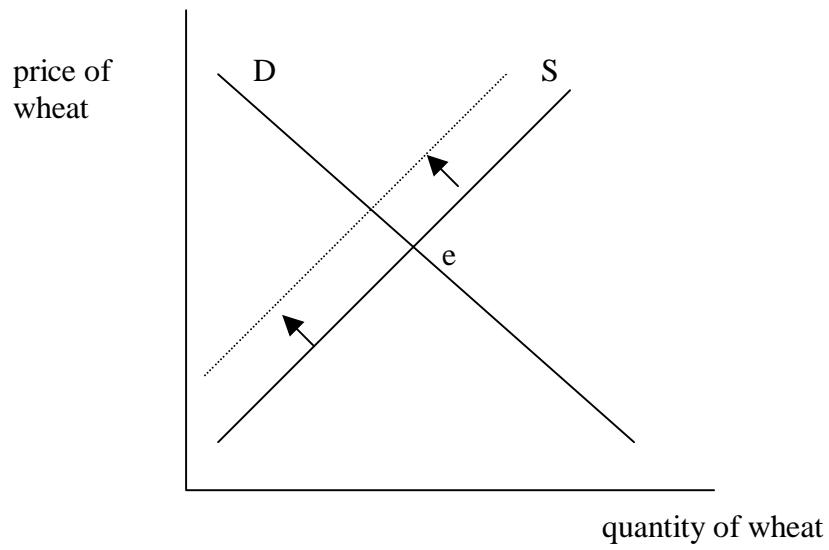


Figure 2 – Market dynamics

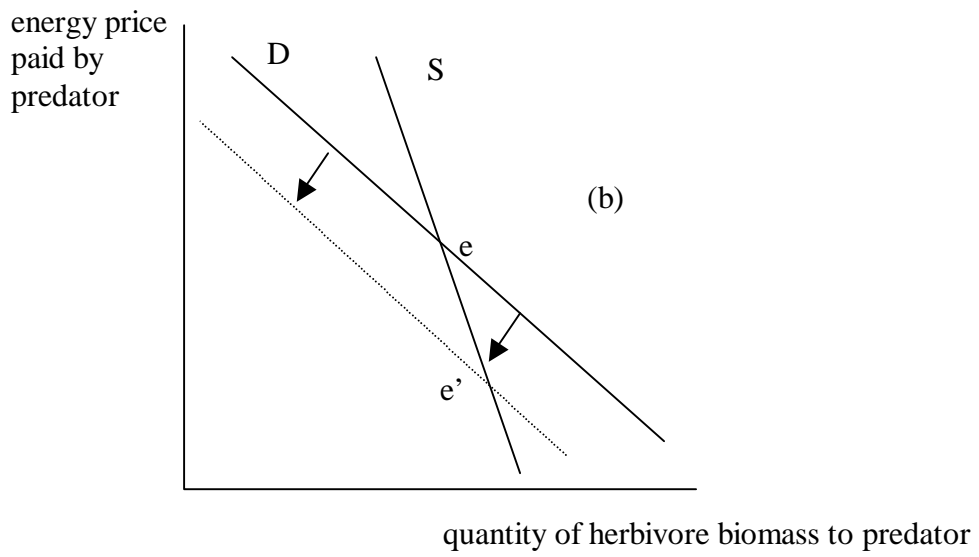
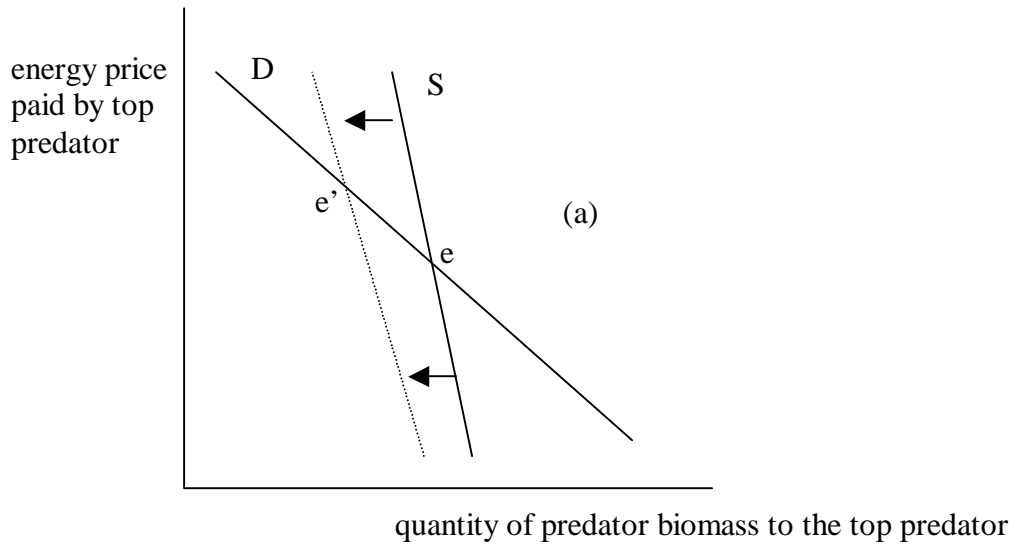


Figure 3 – Two ecological transfers: (a) shows the top predators preying on the predators, and (b) shows the predators preying on the herbivores.

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