Single Species versus Multiple Species Models: The Economic Implications

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ABSTRACT

Ecologists frequently note the importance of modelling entire ecosystems rather than single species, but most bioeconomic models in the current literature focus on a single species. While the mathematical difficulty of multiple species may quickly become overwhelming, sometimes making the single species option necessary, it is important to recognise the significance of the single species assumption to the model results. In this paper, the authors address the economic significance of this assumption through the development of a multiple species model and demonstrate the importance of interrelationships and economic values to the survival of endangered species.

1. INTRODUCTION

Conservation efforts have traditionally been focussed on the identification and preservation of a small number of charismatic species. This approach has increasingly been challenged as our knowledge of the many and varied interactions among species, their habitat, and the environment have improved. While the ecological implications of modelling species in isolation rather than as part of an ecosystem, are well documented (Pimm, 1991; Begon et al., 1996; Milner-Guilland and Mace, 1998), little attention has been paid to the economic implications. This paper seeks to redress this imbalance by exploring the introduction of multiple species into the traditional bioeconomic modelling framework.

The bioeconomic modelling of species extinction has grown out of the literature of fisheries economics. Working from Gordon's (1954) seminal fisheries model, Clark (1973) develops a model to analyse the decision-making of a sole owner seeking to maximise the present value of his harvests. He identifies the conditions under which the owner has an economic incentive to harvest the species to extinction. Clark identifies three conditions that would make such a choice optimal[1]: 1) open access to the resource, 2) a price to harvest cost ratio greater than one, and 3) a low growth rate of the resource relative to the social discount rate. If either the first condition or the last two conditions are met, then resource extinction may occur.

Many extensions have been made to Clark's original model. Clark et al. (1979) study the effects of irreversible capital investment, concluding a short-run situation exists during which a fishery faces an overcapacity of harvesting resources, before leading to a long-run equilibrium situation of optimum sustainable yield. Swanson (1994) recognising that, unlike marine species, terrestrial species compete with humans for the use of land resources, seeks to bring the literature 'onshore' by including land resources as an additional control variable.

Further, such models are increasingly applied to issues of terrestrial conservation. For example, Bulte and van Kooten (1996) offer a model of the African Elephant to analyse the effects of the Convention on International Trade in Endangered Species (CITES) trade ban on optimal elephant stocks for the range state of Kenya. The authors present an empirical model with terms for harvest revenue, tourism revenue and elephant damage to crops and wildlife habitat.

They conclude, as long as the societal discount rate is greater than 3.5 percent (highly likely in the case of a developing nation), a trade ban would result in higher elephant stocks than

[1] Clark is careful to note the distinction between socially optimal, and optimal in terms of present value maximisation to the resource harvester. It is the latter case Clark considers here.

would be likely under a controlled harvest policy. However, their model generates an optimal stock level, irrespective of the discount rate, of 15,700, three hundred less than actual stock at the time of the study. Given the perceived need to devote resources to elephant conservation, and the declining populations in Kenya, this result is somewhat surprising. One must carefully consider exactly what *optimal* means in such a case.

Considering both the harvest and non-harvest case, Skonhoft (1999) analyses the optimal management of species when land use costs, non-consumptive benefits and nuisance costs are taken into account. Skonhoft concludes, in each case, that an increase in the profitability of alternative land use activities (such as farming) will lead to a long-run loss of habitat and consequently animal numbers.

A notable feature of the aforementioned models is their single species focus. Though many authors acknowledge the shortcomings of such an approach (Ragozin and Brown, 1985; Bulte and van Kooten, 1996) the bioeconomic literature remains dominated by single species models. The purpose of this paper is to compare and contrast single versus multiple species bioeconomic models, paying particular attention to the economic implications arising from the misapplication of the single-species case.

The Clark model is briefly reviewed in Section 2 as a base from which to launch the development of our model. The economic theory underlying the multiple species approach is examined in Section 3 with reference to the theory of joint production. The multi-species model is developed in Section 4 and applied to three cases of species interaction: independent, predator-prey and interspecific competition. Finally, some implications of the multiple species approach are drawn in Section 5 and suggestions are made for further research.

2. THE SINGLE SPECIES MODEL

Although the bioeconomic literature had recognised the possibility of harvesting a species to extinction (Smith, 1969; Bachmura, 1971; Gould, 1972), Clark was first to explicitly model such a case and it is his work that has formed the foundation of the subsequent literature.

In a situation in which the owner is seeking to maximise static rent (net revenue) from the resource, Clark determines that in all cases, irrespective of the relative price to the cost of harvest, an optimal positive stock level results. That is, static rent maximisation never leads to extinction. However, when the problem becomes one of maximising the present value of net revenue streams, Clark demonstrates that if the price exceeds the cost of harvest for all stock levels, and the discount rate is sufficiently large, then the potential for extinction exists.

Clark (1973) posits a societal objective function of maximising the present value of the net returns from the resource as follows[2]:

$$\max_{h} \int_0^{\infty} e^{-\delta t}[\, p(h(t))h(t) - c(x(t))h(t)]dt \qquad (1)$$

$$s.t. \quad \dot{x} = F(x(t)) - h(t)$$

where $x(t)$ is the stock level of the species in time t, h(t) is the harvest of the species in time t, p(h(t)) is the inverse demand curve defined as a function of harvest, c(x(t)) is the unit cost of harvest as a function of stock, and δ is the societal discount rate. For convenience of exposition, the time notation will subsequently be suppressed, but will be understood to be implicit in all control and state variables.

Clark applies this problem to an optimal control framework, then derives and manipulates the necessary conditions to arrive at the condition associated with optimal stock levels (x^*) as shown in Equation (2).

$$\delta = F'(x) - \frac{c'(x)h}{p(h) - c(x)} \qquad (2)$$

Equation (2) represents a modified version of the *golden rule* equation common in natural resource applications. The original golden rule, $\delta = F'(x)$, suggests the resource should be maintained at a stock level such that the returns to capital available to the resource owner, δ, are equal to the marginal productivity of the renewable resource stock, $F'(x)$.

In this modified form, Equation (2) implies that returns to the resource are dependent upon two factors: the growth rate of the resource and the cost of harvest (which is a decreasing function of stock, $c'(x) < 0$). This modification therefore increases the effective marginal productivity of the stock relative to the discount rate, making the stock a more attractive investment.

The policy implications are straightforward. Extinction results from low growth rates and high price–cost (of harvest) ratios. Given that policymaker's ability to alter the growth rate of a natural resource is limited, the policy response must focus on the price-cost ratio. As Swanson (1994) points out, this is the mechanism by which policies such as a CITES trade ban works. By effectively removing the value of harvest, policymakers create a more favourable price–cost ratio for the species in question.

[2] For notational consistency with the models below, we use Clark's (1976) interpretation of Clark (1973).

3. DEALING WITH MULTIPLE SPECIES

The model given above presents an unspecified growth function of the renewable resource stock, $F(x)$. This is often assumed to be the logistic growth function first proposed as a population model by P.F. Verholst in 1838 (Clark, 1976):

$$F(x) = rx\left(1 - \frac{x}{K}\right) \tag{3}$$

where r is the intrinsic growth rate of the resource and K is the carrying capacity of the habitat. This growth function in the fishery problem is analogous to the production function in general economic theory.

Production economics literature makes clear the distinction between firms producing single outputs and those producing multiple outputs (Beattie and Taylor, 1985). The function specified above clearly belongs to the former case. However, to the extent that the allocation of land resources for conservation of one species necessarily provides habitat to other species which share that land, conservation management may be more properly viewed as a multiple product production process. To recognise this relationship within the bioeconomic framework it is necessary to specify multiple product production functions.

Within multiple product production, distinction is drawn between joint and non-joint production. Joint production is said to exist when more than one output emerges from a single productive activity. Two classes of joint production are distinguished in the literature: the case where all joint products are desirable, and the case where one product is desirable while another is undesirable (Baumgartner et al, 2001). The latter case is well documented in the ecological economics literature. Early authors, including Johann Heinrich von Thumen, William Jevons and Karl Marx, all address the phenomenon of pollutants arising as joint products of desired goods (Baumgartner, 2000).

While well studied in production economics, the case where all joint products are desirable has received little attention in ecological economics. However, Baumgartner et al (2001) have recently suggested joint production, though not recognised as such, is in fact a fundamental concept in ecology. They argue that ecosystems "…as open, self-organising systems, necessarily take in several inputs and generate several outputs…" (p.367). Although it is by no means the case that all species are at all times desirable, it is a working assumption in this article that the conservation problem is one in which that assumption may hold. Thus, we will not address the case of undesirable species in this work.

A further distinction found in the literature is between allocable and non-allocable factors of production. Allocable factors are those for which the amount of the factor of production used in producing a given output y_1 can be distinguished from the amount of that factor used in producing output y_2 (Beattie and Taylor, 1985).

Where the factor under consideration is conservation land, clearly we have a case of a non-allocable factor. Once a conservation area has been established, the area is freely available for use by each species living within it. The case of joint production with non-allocable factors of production is illustrated in Figure 1,

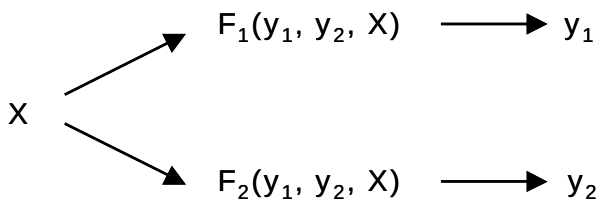

Figure 1. A non-allocable factor of production. (Adapted from: Beattie and Taylor, 1985)

where X represents the total quantity of input (land), and $F_1(\cdot)$ and $F_2(\cdot)$ represent the production functions through which X is converted into outputs y_1 and y_2 (species 1 and 2) respectively.

4. THE MULTIPLE SPECIES MODEL

a. The Generalised Model

In this section, we develop a simple two-species model to demonstrate the effect of adding additional species to the single species bioeconomic framework. Suppose society wishes to maximise the present value of net returns from harvesting both species. The objective function may be specified as:

$$\max_h \int_0^\infty e^{-\delta t}\{[p_1 - c_1(x_1)]h_1 + [p_2 - c_2(x_2)]h_2 - \delta p_L L\} \qquad (4)$$

where subscripts denote species one and two, L is a unit of terrestrial resource (land) upon which the species depends for survival, and p_L is the unit price of a base unit of that land resource. Following Swanson (1994), this land term is multiplied by the social discount rate, δ, to indicate that the returns from our two species must match the opportunity cost of

alternative returns available from use of the same land. For transparency the inverse demand function of the standard bioeconomic model, p(h), has been replaced by fixed prices p_1 and p_2. All other notation is as previously indicated.

The dynamics defining the change in stock of each species are represented by the state equations:

$$\dot{x}_1 = F(x_1, x_2, L) - h_1 \tag{5}$$

$$\dot{x}_2 = G(x_1, x_2, L) - h_2 \tag{6}$$

where $F(x_1, x_2, L)$ and $G(x_1, x_2, L)$ are the joint production functions of species one and two, where the land resource, L, is non-allocable.

Using the Pontryagin necessary conditions for maximisation of this problem, and simplifying the notation by allowing $R_1 = R_1(x_1) = p_1 - c_1(x_1)$ and $R_2 = R_2(x_2) = p_2 - c_2(x_2)$ to represent net revenues from harvest, the following conditions are derived[3]:

$$\delta = \frac{R_1 F_L}{p_L} + \frac{R_2 G_L}{p_L} \tag{7}$$

$$\delta = F_1(x_1, x_2, L) - \frac{c_1'(x_1) F(x_1, x_2, L)}{R_1} + \frac{R_2}{R_1} G_1(x_1, x_2, L) \tag{8}$$

$$\delta = G_2(x_1, x_2, L) - \frac{c_2'(x_2) G(x_1, x_2, L)}{R_2} + \frac{R_1}{R_2} F_2(x_1, x_2, L) \tag{9}$$

We assume throughout that $R_1, R_2 > 0$ for all relevant levels of x_1, x_2, otherwise the cost of harvest would exceed the revenues and no harvest would occur. Equation (7) reflects the impact of the land control term in the objective function, and is a multiple species version of the result found by Swanson (1994). This condition implies that society will allocate land only to the extent that the species supported by it are able to generate a competitive rate of return from their use of the resource. In a single species model, it would appear that this return must be generated entirely by the species under consideration. However, when the conservation of a wilderness area provides benefits to many species, the returns generated by all species may contribute to meeting the required returns from the land resource.

Although we restrict our intention to the two species case, the extension to multiple species will simply lead to additional terms on the RHS, resulting in a further reduction of individual

[3] For the full derivation of these conditions, see the Appendix.

species burden. This relationship holds regardless of the nature of any interdependence between the species.

Equations (8) and (9) are modified golden rule equations for species 1 and 2 respectively, analogous to that shown in Equation (2). Recall that the LHS and the first term on the RHS indicate that the resource must be maintained at a stock level such that the marginal productivities of the resource stocks, F_1 and G_2, equate to the return available from other assets δ. All other terms on the RHS modify that relationship.

The second terms on the RHS of Equations (8) and (9) reflect the stock-dependent harvest costs ($c'(x) < 0$), expressed proportionately to the unit net revenue of harvesting the resource. The only adjustment from the single species case is that the growth functions, $F(x_1, x_2, L)$ and $G(x_1, x_2, L)$, are now potentially interdependent. As before, this term acts to increase the marginal productivity of the resource, making the resource a more attractive investment. While these terms exhibit potential interdependence between species, they arise directly from the harvest activity and are strongly dependent on the ratio of marginal costs to marginal revenues.

The third terms on the RHS of Equations (8) and (9) reflect the biological interdependence of the two species, modified by the relative marginal profitability of each. Each equation indicates that returns for one species are modified by the marginal affect that species has on the other, times the proportional revenue of the other species to the first. Whether this makes a species more or less desirable in the human asset portfolio depends upon both the ecological relationship between the species and the relative values of the species. We shall henceforth refer to these as the *interdependence terms*.

b. Considering Species Interdependence

We consider three cases of species interdependence: (i) independent species, (ii) a predator-prey relationship, and (iii) species competition.

(i) Independent Species

In the independent case, each species' state equation is a function only of its own population and the land resource so that $G_1(x_1, x_2, L) = F_2(x_1, x_2, L) = 0$. Equations (5) and (6) become:

$$\dot{x}_1 = F(x_1, L) - h_1 \tag{10}$$

$$\dot{x}_2 = G(x_2, L) - h_2 . \tag{11}$$

Consequently, the interdependence terms of Equations (8) and (9) become zero, and the conditions revert to a pair of modified golden rule harvest conditions from the standard model.

$$\delta = F_1 - \frac{c_1'(x_1)F(x_1, L)}{R_1} \tag{12}$$

$$\delta = G_2 - \frac{c_2'(x_2)G(x_2, L)}{R_2} \tag{13}$$

In the independent species case, harvest decisions for each species are made without regard to the existence of the other species. In this respect, a two species model would yield the same results as two independently developed single species models is we failed to consider the constraint on returns to land. In a fisheries case, in which there were no returns to land to consider, species independence may be sufficient to justify the use of a single species model. However, for terrestrial conservation, each species is still dependent on the same land input for its production as indicated in Equation (7). Thus, both species still contribute to returns to the land resource even though each species may be harvested as indicated in a single species model. Swanson (1994) makes a compelling argument for considering returns to land in terrestrial species conservation. This model supports that argument and extends it by demonstrating the need to consider all relevant species in an ecosystem, even when they appear to be independent.

(ii) Predator-Prey

The predator-prey relationship is defined as one in which the growth of one species is positively affected by the presence of the second, but in which the growth of the second species is adversely affected by the presence of the first. In the generalised model, this implies $G_1(x_1, x_2, L) < 0,\ F_2(x_1, x_2, L) > 0$ or $G_1(x_1, x_2, L) > 0,\ F_2(x_1, x_2, L) < 0$. Suppose species 1 is a predator ($G_1(x_1, x_2, L) < 0$) and species 2 is its prey ($F_2(x_1, x_2, L) > 0$). Then the interdependence term of Equation (8), works against the predator (makes it less valuable), while the corresponding term in Equation (9), works in favour of the prey species. If both species have a harvest value, the predator, by reducing the growth of its prey, is reducing the potential returns to the land resource. Conversely, the prey is increasing potential returns by increasing the growth of the predator. The magnitudes of these impacts are dependent on the relative value of the two species. We offer two cases: (a)

the predator is of greater value than the prey and (b) the prey is of greater value than the predator.

(a) Predator has greater value ($R_1 > R_2$).

As the value of the predator increases relative to that of the prey, the magnitude of the term working against the predator in Equation (8) is reduced, while the magnitude of the term working in favour of the prey in Equation (9) is increased. This creates a situation in which the relative values are working in favour of both species. At moderate ratios of net revenue, the resource owner has the incentive to maintain healthy positive populations of both species; the predator as a source of harvest revenue, and the prey as both a source of food for the predator and for harvest.

In the extreme case, as the net value of the prey approaches zero, Equation (8) reverts to something similar to the single-species modified golden rule condition and Equation (9) approaches the (unmodified) golden rule result. Interdependencies remain in these equations, however, as the predator is still dependent on the prey for food. The model predicts the relationship we would expect where a high-value predator is harvested and a low-value prey is not, in that significant populations of both stocks are maintained.

(b) Prey has greater value ($R_1 < R_2$).

When the prey is of greater relative value, the magnitude of the term working against the predator in Equation (8) is increased, while simultaneously decreasing the magnitude of the term working in favour of the prey in Equation (9) (as the value of the prey as a food source for the predator is reduced). At modest ratios of net revenue, the owner has incentives to maintain both species, but at smaller equilibrium populations than when the predator has the greater value.

As the harvest value of the predator approaches zero ($R_1 \to 0$), given the prey has some positive net value ($R_2 > 0$), then the resource owner has the incentive to harvest the predator to extinction. This is the behaviour exhibited by livestock owners around the world as they seek to eliminate all predation of their stock, and is a principle cause of the decline of wild predators.

(iii) Competition

The distinguishing characteristic of this case is that each species acts against the interests of the other, so that $G_1(x_1, x_2, L) < 0,\ F_2(x_1, x_2, L) < 0$. One again, the outcome is determined by the relative values of the species. If species 1 is of greater (lesser) value than species 2, then the magnitude of the term working against species 1 in Equation (8) is reduced (increased), and the magnitude of the term working against the second species in Equation (9) is increased (reduced). If competition exists between two species, the resource owner has the incentive to reduce populations of the lower value species, in favour of retaining the species with higher value. At moderate ratios of net revenue, the resource owner has insufficient incentive to exterminate the less valuable species, and populations of both species will be retained.

However, as one species gains significantly greater value than the other, the resource owner has an incentive to harvest the less valued species to extinction, so as to devote all of the land resources to production of the more valuable species. Livestock husbandry is the extreme manifestation of this behaviour.

5. CONCLUSION

While the importance of taking an ecosystem approach to species conservation is well documented in the ecological and conservation biology literatures, the economic implications have been less thoroughly addressed. Working from within the existing bioeconomic framework, we have developed a multiple species model that allows several economic implications to be drawn, and in part illustrates the incentives behind observable human actions.

The model demonstrates that the addition of species to the single species framework spreads the burden of generating a competitive return to land resources across all species, which otherwise may appear to fall solely on an individual species. This may have significant quantitative implications for the estimation of optimal species stocks, such as those calculated by Bulte and van Kooten (1996) for the African Elephant. It further illustrates that this result holds independently of the relationship between the species.

Where interdependencies between species exist, the model demonstrates more complex behavioural relationships. The predator-prey case highlights the importance a species relative value has on its ultimate fate. The case in which the prey is of high value and the predator of little value is particularly revealing. Here the incentive exists for the resource owner to harvest the predator species to extinction. The decline of wild predators throughout the world

can largely be traced to behaviour consistent with that predicted by the model. When the predator is of relatively higher value, the incentives act to preserve both species. Though this case is less common than the former, it can be observed in many areas of the world, such as in African game parks where the presence of predators is critical to the success of the operations.

Relative values also have implications for competing species. In this case each species acts against the economic interest of the other and resource owners have the incentive to reduce stocks of low value species in favour of retaining species of high value, though this tendency is often buffered from extremes by the presence of stock-dependent harvest costs.

An important outcome of the model is that one can use it to infer the conditions under which a single species model may be appropriate, at least in general terms. If species are independent, and either the opportunity cost of capital or the value of wilderness land is very low, then a single species model may yield results similar to that of a multiple species model. In this case the burden on species, as given by Equation (7), is negligible while Equations (8) and (9) become similar to the single species modified golden rule.

Similarly, if the relative value of one species is significantly greater than that of all others in the ecosystem, then a single species model may also approximate the results of a multiple species approach. In this case, the interdependent terms are negligible for all except the species of value. Even when this occurs, the valid use of a single species model is not certain as the ecological interdependencies in the species' growth functions may still introduce additional effects not considered here. Such effects must be considered on a case-by-case basis.

Clearly, in the absence of these conditions, the model demonstrates that the inclusion of at least all economically valuable species in an ecosystem is important. Using single species models where multiple species are economically significant may lead to misleading results and ultimately to incorrect policy decisions.

REFERENCES

Bachmura, F. "The Economics of Vanishing Species." *Natural Resources Journal* 11, no. 4(1971): 674-92.

Baumgartner, S. *Ambivalent Joint Production and the Natural Environment: An Economic and Thermodynamic Analysis*. New York: Physica-Verlag, 2000.

Baumgartner, S. Dyckhoff H. Faber M. Proops J. and Schiller J. "The Concept of Joint Production and Ecological Economics." *Ecological Economics* 36(2001): 365-72.

Beattie, B. and Taylor C. *The Economics of Production*. New York: John Wiley & Sons, 1985.

Begon, M. Harper J. and Townsend C. *Ecology (3rd Ed.)*. Oxford: Blackwell Science , 1996.

Bulte, E. and van Kooten G. "A Note on Ivory Trade and Elephant Conservation." *Environment and Development Economics* 1, no. 4 (1996): 433-43.

Clark, C. "Profit Maximisation and the Extinction of Animal Species." *Journal of Political Economy* (1973): 950-961.

Clark, C. *Mathematical Bioeconomics: The Optimal Management of Renewable Resources*. New York: John Wiley & Sons, 1976.

Clark, C. Clarke F. and Munro G. "The Optimal Exploitation of Renewable Resource Stocks: Problems of Irreversible Investment." *Econometrica* 47, no. 1(1979): 25-47.

Gordon, H. "The Economic Theory of a Common-Property Resource: The Fishery." *The Journal of Political Economy* (1954).

Gould , J. "Extinction of a Fishery by Commercial Exploitation: A Note." *Journal of Political Economy* 80(1972): 1031-39. Cited in Clark, C. "Profit Maximisation and the Extinction of Animal Species." *Journal of Political Economy* (1973): 950-961.

Milner-Guilland, E. and Mace R. *Conservation of Biological Resources*. Oxford: Blackwell Science , 1998.

Pimm, S. *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*. Chicago: The University of Chicago Press, 1991.

Ragozin, D. and Brown G. "Harvest Policies and Nonmarket Valuation in a Predator-Prey System." *Journal of Environmental Economics and Management* 12 (1985): 155-68.

Skonhoft, A. "On the Optimal Exploitation of Terrestrial Animal Species." *Environmental and Resource Economics* 13, no. 1(1999): 45-57.

Smith, V. "On Models of Commercial Fishing." *Journal of Political Economy* 77(1969): 181-98.

Swanson, T. "The Economics of Extinction Revisited and Revised: A Generalised Framework for the Analysis of the Problems of Endangered Species and Biodiversity Losses." *Oxford Economic Papers* 46(1994): 800-821.

APPENDIX — DERIVATION OF EQUATIONS (7, 8, 9)

The societal objective function is:

$$\max_{h} \int_0^{\infty} e^{-\delta t}\{[p_1 - c_1(x_1(t))]h_1(t) + [p_2 - c_2(x_2(t))]h_2(t) - \delta p_L L(t)\}$$
$$s.t.\ \dot{x}_1 = F(x_1(t), x_2(t), L(t)) - h_1(t)$$
$$\dot{x}_2 = G(x_1(t), x_2(t), L(t)) - h_2(t)$$

For notational convenience, the time notation will subsequently be omitted, but will be understood to be implicit in all control and state variables.

The current value Hamiltonian is:

$$H = [p_1 - c_1(x_1) - \lambda_1]h_1 + [p_2 - c_2(x_2) - \lambda_2]h_2 - \delta p_L L + \lambda_1 F(x_1, x_2, L) + \lambda_2 G(x_1, x_2, L) \quad \text{(A1)}$$

The Pontryagin necessary conditions for a maximum are:

Optimality equations

$$\frac{\partial H}{\partial h_1} = p_1 - c_1(x_1) - \lambda_1 = 0 \quad \text{(A2)}$$

$$\frac{\partial H}{\partial h_2} = p_2 - c_2(x_2) - \lambda_2 = 0 \quad \text{(A3)}$$

$$\frac{\partial H}{\partial L} = -\delta p_L + \lambda_1 F_L + \lambda_2 G_L = 0 \quad \text{(A4)}$$

Co-state equations

$$\frac{-\partial H}{\partial x_1} = -[-c_1'(x_1)h_1 + \lambda_1 F_1 + \lambda_2 G_1] = \dot{\lambda}_1 - \delta\lambda_1 \quad \text{(A5)}$$

$$\frac{-\partial H}{\partial x_2} = -[-c_2'(x_2)h_2 + \lambda_1 F_2 + \lambda_2 G_2] = \dot{\lambda}_2 - \delta\lambda_2 \quad \text{(A6)}$$

State equations

$$F(x_1(t), x_2(t), L(t)) - h_1(t) = 0 \quad \text{(A7)}$$

$$G(x_1(t), x_2(t), L(t)) - h_2(t) = 0 \quad \text{(A8)}$$

and the usual transversality and boundary conditions.

Solve Equations (A2) and (A3) for λ_1 and λ_2 respectively

$$\lambda_1 = p_1 - c_1(x_1) \tag{A9}$$

$$\lambda_2 = p_2 - c_2(x_2) \tag{A10}$$

Take d/dt of Equations (A9) and (A10)

$$\dot{\lambda}_1 = -c_1'(x_1)\dot{x}_1 \tag{A11}$$

$$\dot{\lambda}_2 = -c_2'(x_2)\dot{x}_2 \tag{A12}$$

Substitute Equations (A9) and A(10) into A(4)

$$-\delta p_L + [p_1 - c_1(x_1)]F_L + [p_2 - c_2(x_2)]G_L = 0 \tag{A13}$$

Substitute Equations (A9), (A10) , A(11) and A(12) into Equations (A5) and (A6)

$$c_1'(x_1)h_1 - [p_1 - c_1(x_1)]F_1 - [p_2 - c_2(x_2)]G_1 = c_1'(x_1)\dot{x}_1 - \delta[p_1 - c_1(x_1)] \tag{A14}$$

$$c_2'(x_2)h_2 - [p_1 - c_1(x_1)]F_2 - [p_2 - c_2(x_2)]G_2 = c_2'(x_2)\dot{x}_2 - \delta[p_2 - c_2(x_2)] \tag{A15}$$

Assume a system in equilibrium such that all conditions are met simultaneously. Let $\dot{x} = 0$ at equilibrium, by definition, so that $-c_1'(x_1)\dot{x}_1 = 0$ and $-c_2'(x_2)\dot{x}_2 = 0$. Further, let $h_1 = F(x_1, x_2, L)$ and $h_2 = G(x_1, x_2, L)$ at equilibrium from Equations (A7) and (A8). Given these assumptions, solve Equations (A13), (A14) and (A15) for δ.

$$\delta = \frac{[p_1 - c_1(x_1)]F_L}{p_L} + \frac{[p_2 - c_2(x_2)]G_L}{p_L} \tag{A16}$$

$$\delta = F_1 - \frac{c_1'(x_1)F(x_1, x_2, L)}{[p_1 - c_1(x_1)]} + \frac{[p_2 - c_2(x_2)]}{[p_1 - c_1(x_1)]}G_1(x_1, x_2, L) \tag{A17}$$

$$\delta = G_2 - \frac{c_2'(x_2)G(x_1, x_2, L)}{[p_2 - c_2(x_2)]} + \frac{[p_1 - c_1(x_1)]}{[p_2 - c_2(x_2)]}F_2(x_1, x_2, L) \tag{A18}$$

Let unit net revenue from species i be denoted $R_i = [p_i - c_i(x_i)]$ and substitute into (A16), (A17) and (A18).

$$\delta = \frac{R_1 F_L}{p_L} + \frac{R_2 G_L}{p_L} \tag{7}$$

$$\delta = F_1 - \frac{c_1'(x_1)F(x_1, x_2, L)}{R_1} + \frac{R_2}{R_1} G_1(x_1, x_2, L) \tag{8}$$

$$\delta = G_2 - \frac{c_2'(x_2)G(x_1, x_2, L)}{R_2} + \frac{R_1}{R_2} F_2(x_1, x_2, L) \tag{9}$$