

THE STRUCTURE AND EVOLUTION OF COMPETITION-ORGANIZED ECOLOGICAL COMMUNITIES

ROBERT MCKELVEY AND JOSEPH APALOO

1. Introduction. It frequently is asserted that conservation biology can advance only by transcending the current species-by-species approach and refocusing on whole-ecosystem preservation [13]. But a strong scientific basis does not presently exist for carrying out ecosystem viability analyses, and in particular the theory of community ecology seems to be in disarray [3]. Even classical equilibrium co-evolutionary theory [8] which remains the basis for much subsequent work, seems to have dissolved into controversy, with disputes over what had seemed previously to have been settled principles [2, 9].

It is our view that much of this confusion and controversy has resulted from an excessive level of abstraction in the models employed, making it difficult to distinguish between individual and group control mechanisms, and confounding behavioral and evolutionary processes of adaptation.

Our response is to present a more mechanistic, less phenomenological class of models, in which these separate controls and processes are explicitly distinguished. To our knowledge, ours is the first attempt to systematically incorporate both behavioral optimization and strategic evolutionary processes into a single model.

This article is the first of several that we intend to devote to this subject. Here we describe the model precisely and undertake its theoretical analysis.

In a second article we shall apply the analytical results to specific situations, and thereby reexamine classical questions such as competitive exclusion and niche displacement. This enables us to investigate

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such issues in conservation biology as inherent ecological valuation of species.

In a third article, we shall extend the analysis to age-structured populations, thus making contact with the extensive literature on optimal life histories and opening a new avenue between that subject and co-evolutionary theory.

2. A general strategic model of co-evolution. We begin, in the classical way, [5], with a set of differential or difference equations, describing the dynamics of population densities y_m , $m = 1, 2, \dots, M$, for a community of ecologically-interacting species, with evolutionary phenotypic change being characterized through “strategic” reasoning [10]. More specifically, we build on the insights of [2, 4, 7]. We develop and extend these concepts in the present section. Explicit behavioral optimization is postponed to Section 3.

The following notation will be adhered to: an underscored bolded symbol will denote a vector with vector components, a bolded symbol will represent a vector with scalar components and unbolded symbols will be scalars. For simplicity, assume that each species is represented by only a single (vector) phenotype, characterized by a type vector $\underline{\xi}_m = [\xi_m^{(1)}, \xi_m^{(2)}, \dots, \xi_m^{(n)}]$ chosen from Ξ_m , a finite-dimensional phenotype-space. In the case of continuous time, the dynamic equations take the form

$$(2.1) \quad \frac{1}{y_m} \frac{dy_m}{dt} = \gamma_m[\underline{\xi}, \mathbf{y}]$$

with $\gamma_m[\underline{\xi}, \mathbf{y}]$ being the per capita growth rate for species m . It depends on the M -dimensional vector \mathbf{y} of species densities and also on the M -dimensional vector $\underline{\xi}$ of species phenotypes.

At a dynamic equilibrium, the growth rate of each species present is reduced to zero:

$$\gamma_m[\underline{\xi}, \mathbf{y}] = 0, \quad m = 1, 2, \dots, M.$$

Thereby the equilibrium population densities are determined implicitly as functions of $\underline{\xi}$: $y_m = Y_m(\underline{\xi})$. In order for the dynamic equilibrium to be locally stable, it is sufficient that the community matrix (Jacobian)

$$(2.2) \quad \frac{\partial[\gamma_1, \gamma_2, \dots, \gamma_M]}{\partial[y_1, y_2, \dots, y_M]}$$

evaluated at equilibrium, has its eigenvalues confined to the left half-plane.

We now imagine this stable incumbent community to be invaded by small populations of clonally-reproducing mutant phenotypes of the same set of species. We follow the invasion process only through the initial phase, during which the invaders' population densities are too small to significantly impact the per capita growth rates either of incumbents or of other invaders. Thus, invaders' populations grow initially according to dynamic equations of the form

$$(2.3) \quad \frac{1}{z_m} \frac{dz_m}{dt} = g_m[\zeta_m, \underline{\xi}, \mathbf{y}]$$

i.e., dependent on the mutant's species m and phenotype ζ_m , but also on its biological environment $(\underline{\xi}, \mathbf{y})$, induced by the incumbent community.

We shall call $g_m[\zeta_m; \underline{\xi}, \mathbf{y}]$ the individual fitness of an invader of type ζ_m , in the environment $(\underline{\xi}, \mathbf{y})$. (It is essentially the same as Vincent and Brown's [2] fitness-generating function.) Note that if an incumbent community is invaded by a phenotype $\zeta_m = \xi_m$ already present in the community, then

$$(2.4) \quad g_m[\zeta_m, \underline{\xi}, \mathbf{y}] = \gamma_m[\underline{\xi}, \mathbf{y}].$$

If the incumbent population is at ecological equilibrium, then the individual fitness of an invader becomes a function of phenotypes alone:

$$(2.5) \quad G_m[\zeta_m, \underline{\xi}] = g_m[\zeta_m, \underline{\xi}, \mathbf{Y}(\underline{\xi})].$$

G_m depends on the incumbents' phenotypes in two distinct ways: directly through the explicit dependence of g_m upon $\underline{\xi}$, and indirectly through $\mathbf{y} = \mathbf{Y}(\underline{\xi})$. We shall refer to these effects, respectively, as *direct phenotypic dependence* and (indirect) *density dependence*.

Evidently a mutant population of phenotype ζ_m , attempting to invade a dynamically stable incumbent community will immediately be repelled by the community if $G_m[\zeta_m, \underline{\xi}] < 0$; alternatively, its population will grow initially if $G_m[\zeta_m, \underline{\xi}] > 0$. (A formal verification, examining the exact dynamics of the augmented community, was given by A. Hastings [4] and more explicitly by Reed and Stenseth [7]).

In particular, an invader $\zeta_m = \xi_m$ of an incumbent type has $G_m[\xi_m, \underline{\xi}] \equiv 0$, hence is a marginal invader. Differentiating this expression yields, for $\underline{\zeta} = \underline{\xi}$ identically, that (when $m \neq n$, $m \neq k$)

$$(2.6) \quad \frac{\partial G_m}{\partial \zeta_m^{(i)}} + \frac{\partial G_m}{\partial \xi_m^{(i)}} = \frac{\partial G}{\partial \xi_n^{(j)}} = 0;$$

and

$$\frac{\partial^2 G_m}{\partial \xi_k^{(i)} \partial \xi_n^{(j)}} = 0.$$

It is to be understood that not all phenotypes $\zeta_m \in \Xi_m$ are evolutionarily possible for species m ; in general, physico-chemical and biological constraints operate to force trade-offs among the components of ζ_m . We shall assume that *feasible* phenotypes are confined to an *evolutionary possibility set* $\Gamma_m \subseteq \Xi_m$, where Γ_m generally has smaller dimension than Ξ_m and is confined to a local neighborhood of ξ_m .

We also assume that any feasible community $\underline{\zeta}$, with $\zeta_m \in \Gamma_m$ for $m = 1, 2, \dots, M$, and $\underline{\zeta}$ sufficiently close to $\underline{\xi}$, can coexist in a stable equilibrium configuration $Y(\underline{\zeta})$ near to $Y(\underline{\xi})$.

We shall be examining two dual kinds of evolutionary stability:

ES I. An incumbent ecological community $\underline{\xi} \in \Gamma$ will be said to possess a *type I (local) evolutionary stability* when all evolutionarily possible sets of mutants of its members in a suitably small neighborhood will be unable to initially invade: $G_m[\zeta_m, \underline{\xi}] < 0$ for $\zeta_m \in \Gamma_m$ and sufficiently close to ξ_m , $m = 1, 2, \dots, M$.

ES II. A stable ecological community $\underline{\xi} \in \Gamma$ will be said to possess a *type II (local) evolutionary stability* when each of its members ξ_m can successfully achieve initial invasion of all nearby evolutionarily possible equilibrium communities: $G_m[\xi_m; \underline{\zeta}] > 0$ for all $\underline{\zeta} \in \Gamma$ and in sufficiently small neighborhood of $\underline{\xi}$.

We now specialize to the case where, for each species m , the phenotypic space Ξ_m is two-dimensional, and evolutionary possibilities are confined to a one-dimensional curve segment $\Gamma_m : \xi_m = \xi_m(s_m)$ in Ξ_m . We shall focus on a specific phenotype community $\underline{\xi}^*$, with each $\xi_m^* \in \Gamma_m$, to be examined for evolutionary stability.

It will be convenient to choose the curve parameter s_m to be arc length along Γ_m from the reference point ξ_m^* ; thus $\xi_m^* = \xi_m(0)$. Using the vector “dot-product” notation,

$$(2.7) \quad ds_m^2 = d\xi_m \circ d\xi_m.$$

Hence, $\mathbf{u}_m = \{d\xi_m/ds_m \text{ at } s_m = 0\}$ is a unit vector, tangent to Γ_m at $s_m = 0$, and pointing in the direction of increasing s_m .

A second unit vector \mathbf{v}_m is defined to be perpendicular to \mathbf{u}_m and such that $[\mathbf{u}_m, \mathbf{v}_m]$ is a right-handed coordinate system in Ξ_m . As usual [11], the curvature of Γ_m , is defined as

$$\kappa_m = \frac{d\theta_m}{ds_m},$$

where the angle-of-turn θ_m along the curve is measured with respect to this right-handed system. Since

$$(2.8) \quad \frac{d^2\xi_m}{ds_m^2} \circ \frac{d\xi_m}{ds_m} = 0,$$

therefore $d^2\xi_m/ds_m^2$ is parallel to \mathbf{v}_m , and indeed [11]

$$(2.9) \quad \frac{d^2\xi_m}{ds_m^2} = \kappa_m \mathbf{v}_m.$$

With these, we may reformulate the conditions for the phenotypic community $\xi_1, \xi_2, \dots, \xi_M$ to be evolutionarily stable. For notational clarity, let us use $\xi_m = \xi_m(s_m)$ to denote incumbent variation along Γ_m and $\zeta_m = \xi_m(\sigma_m)$ to denote invader variation along this same curve. We may then define

$$G_m^*[\sigma_m, \mathbf{s}] = G[\xi_m(\sigma_m); \xi_1(s_1), \xi_2(s_2), \dots, \xi_M(s_M)].$$

Note that, since $G_m^*[\sigma_m, \mathbf{s}] \equiv 0$ when $\sigma = \mathbf{s}$ (for $k \neq m, k \neq n$)

$$(2.10) \quad \frac{\partial G_m^*}{\partial \sigma_m} = -\frac{\partial G_m^*}{\partial s_m},$$

and

$$(2.11) \quad \frac{\partial G_m^*}{\partial s_n} = \frac{\partial^2 G_m^*}{\partial s_k \partial s_n} = 0.$$

ES I. Necessary conditions for the incumbent community $\underline{\xi}^$ to be stable against local invasion are:

$$(2.12) \quad 0 = \frac{\partial G_m^*}{\partial \sigma_m} = \sum_j \frac{\partial G_m}{\partial \zeta_m^{(j)}} \mathbf{u}_m^{(j)};$$

$$(2.13) \quad 0 \geq \frac{\partial^2 G_m^*}{\partial \sigma_m^2} = \sum_j \sum_i \frac{\partial^2 G_m}{\partial \zeta_m^{(j)} \partial \zeta_m^{(i)}} \mathbf{u}_m^{(j)} \mathbf{u}_m^{(i)} + \kappa_m \sum_j \frac{\partial G_m}{\partial \zeta_m^{(j)}} \mathbf{v}_m^{(j)}.$$

ES II. Necessary conditions for the invadability by members of $\underline{\xi}^$ of nearby incumbent communities are

$$(2.14) \quad 0 = \frac{\partial G_m^*}{\partial s_m} = \sum_i \frac{\partial G_m}{\partial \xi_m^{(i)}} \mathbf{u}_m^{(i)};$$

$$(2.15) \quad 0 \leq \frac{\partial^2 G_m^*}{\partial s_m^2} = \sum_i \sum_j \frac{\partial^2 G_m}{\partial \xi_m^{(i)} \partial \xi_m^{(j)}} \mathbf{u}_m^{(i)} \mathbf{u}_m^{(j)} + \kappa_m \sum_i \frac{\partial G_m}{\partial \xi_m^{(i)}} \mathbf{v}_m^{(i)}.$$

These conditions have a direct geometrical interpretation. Note that the first-order conditions have the same content for both ES I and II: Both require Γ_m to be orthogonal to the gradient ∇G_m of G_m with respect to ξ_m . (However, the second order conditions in general will not be equivalent.) In view of this fact, it is appropriate, in examining both dual stability concepts, to choose \mathbf{v}_m to be in the direction of ∇G_m and then to complete $[\mathbf{u}_m, \mathbf{v}_m]$ to be a right-handed coordinate system.

3. The ecological competition model: Behavioral adaptation. We now explore the ecological-evolutionary community model more thoroughly, illustrating general principles with a specific model of competition. Like a few earlier models (e.g., Lawlor and Smith [5], Taper and Case [12], and Abrams [1]), we explicitly model the population dynamics of prey species, interacting with each other and with

their predators. However, unlike the earlier models, we specify optimal *behavioral* responses, by individual predators to their current ecological environment, as well as allowing for strategic phenotypic changes over evolutionary time. Taken together, these features allow a somewhat more mechanistic, less phenomenological, description, and permit a closer examination of the interplay between ecological and evolutionary processes.

Consider, then, a community of M prey species R_1, R_2, \dots, R_M , with respective population densities $\mathbf{x} = [x_1, x_2, \dots, x_M]$. These grow demographically, possibly interacting with one another, and are being harvested by predators. Their population dynamics are given by

$$(3.1) \quad \frac{dx_m}{dt} = F_m(\mathbf{x}) - H_m \quad \text{for } m = 1, 2, \dots, M$$

with F_m the growth/interaction term and H_m the harvest.

The total harvest H_m of prey species R_m is the sum of the separate harvests by individuals, belonging to a variety of predator species P_ζ , with $\zeta = \alpha, \beta, \dots$. Each individual predator is assumed to be able to target a specific prey species R_m at will, with harvest return to individual effort $e_{\zeta m}$ given by

$$(3.2) \quad h_{\zeta m} = Q_{\zeta m}(x_m) S_{\zeta m}(e_{\zeta m}).$$

Here Q and S are monotone increasing functions with nonincreasing returns to scale. In the simplest case, $h_{\zeta m} = q_{\zeta m} \cdot x_m \cdot e_{\zeta m}$, with the constant $q_{\zeta m}$ called the *catchability*. Thus total harvest is

$$(3.3) \quad H_m = \sum_{\zeta} h_{\zeta m} N_{\zeta}$$

where N_{ζ} is the population density of predator species P_{ζ} .

The individual predator has the ability to choose total effort and effort distribution $\mathbf{e}_{\zeta} = [e_{\zeta 1}, e_{\zeta 2}, \dots, e_{\zeta M}]$ across the prey species:

$$(3.4) \quad e_{\zeta} = e_{\zeta 1} + e_{\zeta 2} + \dots + e_{\zeta M}.$$

This he will do so as to maximize his net energy return function $\pi_{\zeta}(e_{\zeta}, \mathbf{x})$, given his current biotic environment \mathbf{x} . For the time being,

we shall assume that π_ζ is the same function for all individuals of the same species P_ζ , and is of the form

$$(3.5) \quad \pi_\zeta[\mathbf{e}_\zeta, \mathbf{x}] = \sum_{m=1}^M p_{\zeta m} h_{\zeta m}[x_m, e_{\zeta m}] - C_\zeta[e_\zeta]$$

where $p_{\zeta m}$ is the unit energy value of harvest and C_ζ is its total energy cost.

A necessary condition for a maximum of π_ζ is given by the marginal rule

$$(3.6) \quad p_{\zeta m} Q_{\zeta m}(x_m) = \frac{C'_\zeta[e_\zeta]}{S'_{\zeta m}[e_{\zeta m}]}, \quad \text{for } m = 1, 2, \dots, M.$$

Here, prime denotes differentiation.

Under a wide range of conditions (including those described below) the marginal rule, for given \mathbf{x} , will determine a unique optimal effort vector $\mathbf{E}_\zeta(\mathbf{x})$, which maximizes π_ζ , and the relation between \mathbf{x} and \mathbf{E}_ζ will be one-to-one. Thus, solving (3.6) for \mathbf{E}_ζ allows expressing optimal π_ζ as a function of \mathbf{x} alone:

$$\Pi_\zeta^*(\mathbf{x}) = \pi_\zeta[\mathbf{E}_\zeta(\mathbf{x}), \mathbf{x}].$$

Alternatively, eliminating \mathbf{x} yields the individual predator's optimal energy production function:

$$(3.7) \quad \begin{aligned} \Pi_\zeta[e_\zeta] &= \sum_{m=1}^M S_{\zeta m}[e_{\zeta m}] \frac{C'_\zeta[e_\zeta]}{S'_{\zeta m}[e_{\zeta m}]} - C_\zeta[e_\zeta] \\ &= e_\zeta C'_\zeta(e_\zeta) \left[\sum_{m=1}^M \sigma_{\zeta m}(e_{\zeta m}) \theta_{\zeta m} - \kappa_\zeta(e_\zeta) \right]. \end{aligned}$$

Here $\theta_{\zeta m} = e_{\zeta m}/e_\zeta$ so that $\sum_m \theta_{\zeta m} = 1$ and $\sigma_{\zeta m}$ and κ_ζ are effort elasticities for, respectively, specific yield $S_{\zeta m}(e_{\zeta m})$ and cost $C_\zeta(e_\zeta)$;

$$(3.8) \quad \sigma_{\zeta m} = \frac{de_{\zeta m}/e_{\zeta m}}{dS_{\zeta m}/S_{\zeta m}}; \quad \kappa_{\zeta m} = \frac{de_\zeta/e_\zeta}{dC_\zeta/C_\zeta}.$$

See [6].

In a convenient special case, $\sigma_{\zeta m}$ is taken to be a constant, larger than 1, so that both marginal yield $S'_{\zeta m}$ and average yield $S_{\zeta m}/e_{\zeta m}$ are monotone increasing with diminishing returns. Also κ_{ζ} is taken to be linear and decreasing with e_{ζ} :

$$\kappa_{\zeta}(e_{\zeta}) = \kappa_{\zeta}^{(0)} - \kappa_{\zeta}^{(1)} e_{\zeta}; \quad \text{with} \quad \kappa_{\zeta}^{(0)} > 1, \kappa_{\zeta}^{(1)} > 0 \text{ being constants.}$$

From this, the marginal cost C'_{ζ} and average cost C_{ζ}/e_{ζ} curves are *u*-shaped, and intersect where average cost is a minimum.

It follows that any biotic environment \mathbf{x} elicits a unique optimal effort response $\mathbf{e}_{\zeta} = \mathbf{E}_{\zeta}(\mathbf{x})$ and corresponding energy production at a point on the optimal energy yield curve

$$(3.9) \quad \pi_{\zeta} = \Pi_{\zeta}[\mathbf{E}_{\zeta}(\mathbf{x})] = \Pi_{\zeta}^*[\mathbf{x}].$$

Predator populations are assumed to grow at the per capita rate Π_{ζ} , with population dynamics assuming the form

$$(3.10) \quad \frac{1}{N_{\zeta}} \frac{dN_{\zeta}}{dt} = \Pi_{\zeta}[\mathbf{E}_{\zeta}(\mathbf{x})].$$

Thus, over time, the predator populations adjust until, at dynamic equilibrium $\Pi_{\zeta} = 0$. At the same time, the prey species populations are affected by the changing harvest intensity, so that at dynamic equilibrium

$$(3.11) \quad F_m(\mathbf{x}) = H_m(x_m, \mathbf{N}) = \sum_{\zeta} h_{\zeta m}[\mathbf{E}_{\zeta}(\mathbf{x})] N_{\zeta}, \quad \zeta = \alpha, \beta, \dots$$

Coexistence of predator species in ecological equilibrium requires finding a prey population vector \mathbf{x} such that $\Pi_{\zeta}[\mathbf{E}_{\zeta}(\mathbf{x})] = 0$ for each predator species ζ . In general, no more than M such hypersurfaces can intersect simultaneously in \mathbf{x} -space. Thus, no more than M predator species can coexist on M prey species. The possibilities are further limited by the requirement that (3.11) must be solvable for positive values of all N_{ζ} .

4. The co-evolutionary competition system. We now examine the competition model of Section 3 to determine its possible evolution

in the context of the general co-evolutionary principles of Section 2. We derive the detailed formulas for coexistence and co-evolutionary stability (ES I and ES II) against mutant strains of all species, as a basis for subsequently inferring qualitative biological principles concerning evolutionary processes.

4a. *Single incumbent-single local invader.* We assume that both incumbent and invader are of the same species, say $\zeta = \alpha$, and accordingly shall omit the species subscript in all formulas below. The incumbent's phenotype is a vector in Ξ -space; we denote it by \mathbf{v} . We assume that both total cost C and specific yield S_m are explicitly functions of phenotype \mathbf{v} , as well as of effort:

$$C = C(E, \mathbf{v}); \quad S_m(E_m, \mathbf{v}), m = 1, 2, \dots, M.$$

We shall also specialize to the case where

$$Q_m(x_m) = q_m \cdot x_m \quad \text{and} \quad F_m(\mathbf{x}) = x_m f_m(\mathbf{x}).$$

Fitness for the incumbent is then

$$\Pi = \sum_m p_m \cdot q_m \cdot x_m \cdot S_m(E_m, \mathbf{v}) - C(E, \mathbf{v}) = 0,$$

with \mathbf{E} determined by the marginal rules

$$(4.1) \quad p_m \cdot q_m \cdot x_m \cdot S'_m(E_m, \mathbf{v}) = C'(E, \mathbf{v}), \quad m = 1, 2, \dots, M.$$

Here the prime continues to denote differentiation by effort. Eliminating \mathbf{x} from Π with the aid of these equations yields

$$(4.2) \quad \Pi = E \cdot C'(E, \mathbf{v}) \cdot \left\{ \sum_m \sigma_m \theta_m - \kappa \right\} \equiv 0.$$

Ecological equilibrium for each prey species yields

$$(4.3) \quad N \cdot q_m \cdot S_m(E_m, \mathbf{v}) = f_m(\mathbf{x}).$$

Combining with (4.1) and eliminating N yields

$$(4.4) \quad \frac{p_m x_m f_m(\mathbf{x})}{\theta_m \cdot \sigma_m} = \text{constant} = NEC'(E, \mathbf{v})$$

independent of m , $m = 1, 2, \dots, M$.

Equations (4.1)–(4.4) determine the incumbent system: \mathbf{x} , N and \mathbf{E} .

We denote the invader's phenotype by $\mathbf{v}^\#$, its equilibrium effort vector by $\mathbf{E}^\#$, and its individual fitness by $\Pi^\#$. We assume that an invader's fitness is explicitly influenced by the vector \mathbf{x} of incumbent prey populations, but not explicitly by the incumbent predator's population or phenotype. Thus, we are assuming exploitation competition but not direct interference competition. (However, see below.)

The invader accepts \mathbf{x} as given and undertakes to optimize his effort accordingly. His marginal rule

$$p_m \cdot q_m \cdot x_m \cdot S'_m(\mathbf{E}_m^\#, \mathbf{v}^\#) = C'(\mathbf{E}^\#, \mathbf{v}^\#), \quad m = 1, 2, \dots, M$$

determines $\mathbf{E}_m^\#[\mathbf{x}, \mathbf{v}^\#]$. His resulting fitness is:

$$\begin{aligned} \Pi^\# &= \sum_m p_m \cdot q_m \cdot x_m \cdot S_m(\mathbf{E}_m^\#, \mathbf{v}^\#) - C(\mathbf{E}^\#, \mathbf{v}^\#), \\ (4.5) \quad &= \mathbf{E}^\# \cdot C'(\mathbf{E}^\#, \mathbf{v}^\#) \cdot \left\{ \sum_m \sigma_m^\# \theta_m^\# - \kappa^\# \right\}, \end{aligned}$$

which, through $\mathbf{E}^\#[\mathbf{x}, \mathbf{v}^\#]$, is a function of \mathbf{x} as well as $\mathbf{v}^\#$.

Thus $\Pi^\#$ is density dependent but is not directly dependent on the incumbent's phenotype. (Note, however, that such direct interference competition could be modeled easily, most simply by making catchability q_m dependent upon incumbent predators' density and phenotype.)

4b. In order to apply the stability criteria of Section 2, we must calculate first and second variations in $\Pi^\#$ with respect to phenotype changes for both incumbent and invader. Notationally, we shall denote the partial derivative with respect to the i th component of \mathbf{v} by $\partial/\partial v_i$ or, more simply, by ∂_i . Similarly, partials with respect to the i th component of $\mathbf{v}^\#$ will be denoted $\partial/\partial v_i^\#$ or, more simply, by $\partial_i^\#$. Note that these partials are needed, and will be recorded, only for the particular circumstance that $\mathbf{v}^\# = \mathbf{v}$. The calculations are straightforward but will be omitted and the proofs will be provided by the authors upon request.

First variation.

$$\begin{aligned}
 (4.6) \quad -\partial_i \Pi^\# &= \partial_i^\# \Pi^\# \\
 &= EC'(E, \mathbf{v}) \left[\sum_m \frac{\sigma_m \theta_m \partial_i S_m(\cdot, \mathbf{v})}{S_m(E_m, \mathbf{v})} - \frac{\kappa \partial_i C(\cdot, \mathbf{v})}{C(E, \mathbf{v})} \right]
 \end{aligned}$$

and

$$(4.7) \quad 0 = \partial_i \Pi = EC'(E, \mathbf{v}) \left[\sum_m \frac{\theta_m \sigma_m \partial_i x_m}{x_m} \right] = -\partial_i \Pi^\#.$$

Here $\partial_i C(\cdot, \mathbf{v})$ denotes partial differentiation by the i th component of the explicitly shown \mathbf{v} , with the first argument of C , namely E , being represented by a dot to indicate that it is being held constant.

Put $E_m^* = E_m - E_m^\#$ and $E^* = E - E^\#$. Then

$$(4.8) \quad \partial_i^\# E_m^\# = -\partial_i^\# E_m^* = \partial_i E_m^*$$

and the marginal rules yield, for $m = 1, 2, \dots, M$,

$$\begin{aligned}
 (4.9) \quad \{S''(E_m, \mathbf{v}) \cdot \partial_i E_m^* + \partial_i S_m(\cdot, \mathbf{v})\} \frac{\sigma_m \theta_m}{S_m(E_m, \mathbf{v})} \\
 = \{C''(E, \mathbf{v}) \cdot \partial_i E^* + \partial_i C'(\cdot, \mathbf{v})\} \frac{\kappa}{C(E, \mathbf{v})}
 \end{aligned}$$

and

$$\begin{aligned}
 (4.10) \quad \frac{\partial_i x_m}{x_m} + \{S_m''(E_m, \mathbf{v}) \partial_i E_m + \partial_i S_m(\cdot, \mathbf{v})\} \frac{\sigma_m \theta_m}{S_m(E_m, \mathbf{v})} \\
 = \{C''(E, \mathbf{v}) \cdot \partial_i E + \partial_i C'(\cdot, \mathbf{v})\} \frac{\kappa}{C(E, \mathbf{v})}.
 \end{aligned}$$

Finally, the prey equilibrium equations yield, for $m = 1, 2, \dots, M$,

$$\begin{aligned}
 (4.11) \quad \frac{\partial_i N}{N} + \left[\frac{S_m'(E_m, \mathbf{v})}{S_m(E_m, \mathbf{v})} \partial_i E_m + \frac{\partial_i S_m(\cdot, \mathbf{v})}{S_m(E_m, \mathbf{v})} \right] \\
 = \sum_n \left[\frac{(\partial f_m / \partial x_n)}{f_m} \partial_i x_n \right].
 \end{aligned}$$

Second variation.

$$\begin{aligned}
 \partial_i^\# \partial_j^\# \Pi^\# &= EC'(E, \mathbf{v}) \left\{ \sum_m \sigma_m \theta_m \frac{\partial_j S'_m(\cdot, \mathbf{v})}{S_m(E_m, \mathbf{v})} \partial_i^\# E_m^\# \right. \\
 &\quad \left. - \kappa \frac{\partial_j C'(\cdot, \mathbf{v})}{C(E, \mathbf{v})} \partial_i^\# E^\# \right\} \\
 (4.12) \quad &+ EC'(E, \mathbf{v}) \left\{ \sum_m \sigma_m \theta_m \frac{\partial_i \partial_j S_m(\cdot, \mathbf{v})}{S_m(E_m, \mathbf{v})} \right. \\
 &\quad \left. - \kappa \frac{\partial_i \partial_j C(\cdot, \mathbf{v})}{C(E, \mathbf{v})} \right\}
 \end{aligned}$$

and

$$\begin{aligned}
 -\partial_i \partial_j \Pi^\# &= EC'(E, \mathbf{v}) \sum_m \sigma_m \theta_m \left\{ \frac{(\partial_j x_m / x_m)(S'_m(E_m, \mathbf{v}))}{S_m(E_m, \mathbf{v})} \partial_i E_m^* \right. \\
 &\quad \left. + \frac{\partial_i x_m}{x_m} \left[\frac{\partial_j S'_m(\cdot, \mathbf{v})}{S_m(E_m, \mathbf{v})} \right] + \frac{(\partial_j x_m / x_m)(\partial_i S_m(\cdot, \mathbf{v}))}{S_m(E_m, \mathbf{v})} \right\} \\
 &+ EC'(E, \mathbf{v}) \left\{ \sum_m \sigma_m \theta_m \left[\frac{\partial_j S'_m(\cdot, \mathbf{v})}{S_m(E_m, \mathbf{v})} \right] \partial_i E_m \right. \\
 &\quad \left. - \kappa \left[\frac{\partial_j C'(\cdot, \mathbf{v})}{C(E, \mathbf{v})} \right] \partial_i E \right\} \\
 &+ EC'(E, \mathbf{v}) \left\{ \sum_m \sigma_m \theta_m \frac{\partial_i \partial_j S_m(\cdot, \mathbf{v})}{S_m(E_m, \mathbf{v})} \right. \\
 &\quad \left. - \kappa \left[\frac{\partial_i \partial_j C(\cdot, \mathbf{v})}{C(E, \mathbf{v})} \right] \right\}.
 \end{aligned}$$

4c. *Multiple incumbents-multiple invaders.* As pointed out in Section 2, one needs to calculate variations of $\Pi_\zeta^\#$ only with respect to $\partial_{\zeta j}$ and $\partial_{\zeta j}^\#$, not with respect to $\partial_{\eta j}$ or $\partial_{\eta j}^\#$ for $\zeta \neq \eta$. However, a linkage among prey species exists through the prey equilibrium equations:

$$(4.13) \quad \sum_{\zeta} q_{\zeta m} S_{\zeta m}(E_{\zeta m}, \mathbf{v}_{\zeta}) N_{\zeta} = f_m(\mathbf{x}).$$

Differentiating this yields

$$\begin{aligned} \sum_{\zeta} q_{\zeta m} \{ S'_{\zeta m}(E_{\zeta m}, \mathbf{v}_{\zeta}) (\partial_{\alpha i} E_{\zeta m}) \cdot N_{\zeta} + S_{\zeta m}(E_{\zeta m}, \mathbf{v}_{\zeta}) (\partial_{\alpha i} N_{\zeta}) \} \\ + q_{\alpha m} \partial_{\alpha i} S_{\alpha m}(\cdot, \mathbf{v}_{\alpha}) N_{\alpha} = \sum_n \frac{\partial f_m}{\partial x_n} \partial_{\alpha i} x_n. \end{aligned}$$

5. Summary and conclusions. The equations derived in Sections 3 and 4 are logically complete and form a close, solvable system. However, beyond generalities, drawing biological implications will require making specific biological assumptions, notably about effort costs and yields and about biologically plausible evolutionary constraints and trade-offs. These matters will be taken up in detail in the second article of this series.

APPENDIX

Single incumbent/single invader. For the incumbent, individual fitness is

$$(A1) \quad \Pi = \sum_m p_m \cdot q_m \cdot x_m \cdot S_m(E_m, \mathbf{v}) - C(E, \mathbf{v}) \equiv 0,$$

with effort determined by the marginal rules

$$(A2) \quad p_m \cdot q_m \cdot x_m \cdot S'_m(E_m, \mathbf{v}) = C'(E, \mathbf{v}), \quad m = 1, 2, \dots, M.$$

Eliminating \mathbf{x} as in Section 4,

$$(A3) \quad \Pi = E \cdot C'(E, \mathbf{v}) \cdot \left\{ \sum_m \sigma_m \theta_m - \kappa \right\} \equiv 0,$$

where σ_m , θ_m and κ are as defined in Section 3.

From Section 4, predator population size is given by

$$(A4) \quad N \cdot q_m \cdot S_m(E_m, \mathbf{v}) = f_m(\mathbf{x})$$

and eliminating N yields

$$(A5) \quad \frac{p_m x_m f_m(\mathbf{x})}{\theta_m \cdot \sigma_m} = \text{constant} = NEC'(E, \mathbf{v}).$$

For the solitary invader, \mathbf{x} is accepted from the incumbent population and fitness is

$$(A6) \quad \Pi^\# = \sum_m p_m \cdot q_m \cdot x_m \cdot S_m(E_m^\#, \mathbf{v}^\#) - C(E^\#, \mathbf{v}^\#),$$

$$(A7) \quad = E^\# \cdot C'(E^\#, \mathbf{v}^\#) \cdot \left\{ \sum_m \sigma_m^\# \theta_m^\# - \kappa^\# \right\},$$

as similarly obtained above with effort determined by the marginal rules

$$(A8) \quad p_m \cdot q_m \cdot x_m \cdot S'_m(E_m^\#, \mathbf{v}^\#) = C'(E^\#, \mathbf{v}^\#), \quad m = 1, 2, \dots, M.$$

Evolution: First variation.

1) *Varying the invader's phenotype.*

$$\begin{aligned} \partial_i^\# \Pi^\# &= \sum_m p_m q_m x_m [S'_m(E_m^\#, \mathbf{v}^\#) \partial_i^\# E_m^\# + \partial_i^\# S_m(., \mathbf{v}^\#)] \\ &\quad - [C'(E^\#, \mathbf{v}^\#) \partial_i^\# E^\# + \partial_i^\# C(., \mathbf{v}^\#)] \\ (A9) \quad &= \sum_m p_m q_m x_m \partial_i^\# S_m(., \mathbf{v}^\#) - \partial_i^\# C(., \mathbf{v}^\#) \\ &= C'(E^\#, \mathbf{v}^\#) \left[\sum_m \frac{\partial_i^\# S_m(., \mathbf{v}^\#)}{S'_m(E_m^\#, \mathbf{v}^\#)} - \frac{\partial_i^\# C(., \mathbf{v}^\#)}{C'(E^\#, \mathbf{v}^\#)} \right] \\ (A10) \quad &= E^\# C'(E^\#, \mathbf{v}^\#) \left[\sum_m \frac{\sigma_m \theta_m \partial_i^\# S_m(., \mathbf{v}^\#)}{S_m(E_m^\#, \mathbf{v}^\#)} - \frac{\kappa \partial_i^\# C(., \mathbf{v}^\#)}{C(E^\#, \mathbf{v}^\#)} \right] \end{aligned}$$

and from the marginal rule (A8)

$$\begin{aligned} (A11) \quad p_m q_m x_m [S''_m(E_m^\#, \mathbf{v}^\#) \partial_i^\# E_m^\# + \partial_i^\# S'_m(., \mathbf{v}^\#)] \\ = [C''(E^\#, \mathbf{v}^\#) \partial_i^\# E^\# + \partial_i^\# C'(., \mathbf{v}^\#)] \end{aligned}$$

or

$$(A12) \quad \left[\frac{S_m''(E_m^\#, \mathbf{v}^\#)}{S'(E_m^\#, \mathbf{v}^\#)} \right] \partial_i^\# E_m^\# + \frac{\partial_i^\# S_m'(\cdot, \mathbf{v}^\#)}{S'(E_m^\#, \mathbf{v}^\#)} \\ = \left[\frac{C''(E^\#, \mathbf{v}^\#)}{C'(E^\#, \mathbf{v}^\#)} \right] \partial_i^\# E^\# + \frac{\partial_i^\# C'(\cdot, \mathbf{v}^\#)}{C'(E^\#, \mathbf{v}^\#)}$$

when $\mathbf{v}^\# = \mathbf{v}$ these become

$$(A13) \quad \partial_i^\# \Pi^\# = C'(E, \mathbf{v}) \left[\sum_m \frac{\partial_i S_m(\cdot, \mathbf{v})}{S_m'(E_m, \mathbf{v})} - \frac{\partial_i C(\cdot, \mathbf{v})}{C'(E, \mathbf{v})} \right] \\ = EC'(E, \mathbf{v}) \left[\sum_m \frac{\sigma_m \cdot \theta_m \cdot \partial_i S_m(\cdot, \mathbf{v})}{S_m(E_m, \mathbf{v})} - \frac{\kappa \cdot \partial_i C(\cdot, \mathbf{v})}{C(E, \mathbf{v})} \right]$$

and from (A12)

$$(A14) \quad \left[\frac{S_m''(E_m, \mathbf{v})}{S'(E_m, \mathbf{v})} \right] \partial_i^\# E_m^\# + \frac{\partial_i S_m'(\cdot, \mathbf{v})}{S'(E_m, \mathbf{v})} \\ = \left[\frac{C''(E, \mathbf{v})}{C'(E, \mathbf{v})} \right] \partial_i^\# E^\# + \frac{\partial_i C'(\cdot, \mathbf{v})}{C'(E, \mathbf{v})}.$$

Note that $\partial_i^\# (E_m - E_m^\#) = -\partial_i^\# E_m^\#$ since $\partial_i^\# E_m = 0$.

2) *Varying the incumbent phenotype.*

$$(A15) \quad \partial_i \Pi = \sum_m p_m q_m [\partial_i x_m S_m(E_m, \mathbf{v}) + x_m S_m'(E_m, \mathbf{v}) \partial_i E_m + x_m \partial_i S_m(\cdot, \mathbf{v})] \\ - [C'(E, \mathbf{v}) \partial_i E + \partial_i C(\cdot, \mathbf{v})] \\ = \sum_m p_m q_m [\partial_i x_m S_m(E_m, \mathbf{v}) + x_m \partial_i S_m(\cdot, \mathbf{v})] - \partial_i C(\cdot, \mathbf{v}) \\ = EC' \left[\sum_m \sigma_m \cdot \theta_m \cdot \left[\frac{\partial_i x_m}{x_m} + \frac{\partial_i S_m(\cdot, \mathbf{v})}{S_m(E_m, \mathbf{v})} \right] - \frac{\kappa \cdot \partial_i C(\cdot, \mathbf{v})}{C(E, \mathbf{v})} \right]$$

$$\begin{aligned}
\partial_i \Pi^\# &= \sum_m p_m q_m \left[\partial_i x_m S_m(E_m^\#, \mathbf{v}^\#) + x_m S'_m(E^\#, \mathbf{v}^\#) \partial_i E_m^\# \right] \\
&\quad - C'(E^\#, \mathbf{v}^\#) \partial_i^\# E^\# \\
(A16) \quad &= \sum_m p_m q_m \partial_i x_m S_m(E_m^\#, \mathbf{v}^\#) \\
(A17) \quad &= E^\# C'(E^\#, \mathbf{v}^\#) \sum_m \sigma_m^\# \theta_m^\# \frac{\partial_i x_m}{x_m}.
\end{aligned}$$

Invader's and incumbent's marginal rule then give

$$\begin{aligned}
(A18) \quad p_m q_m [\partial_i x_m S'_m(E_m, \mathbf{v}) + x_m S''_m(E_m, \mathbf{v}) \partial_i E_m \\
+ x_m \partial_i S'_m(., \mathbf{v})] - [C''(E, \mathbf{v}) \partial_i E + \partial_i C'(., \mathbf{v})]
\end{aligned}$$

$$\begin{aligned}
(A19) \quad p_m q_m [\partial_i x_m S'_m(E_m^\#, \mathbf{v}^\#) + x_m S''_m(E^\#, \mathbf{v}^\#) \partial_i E_m^\#] \\
= C''(E, \mathbf{v}) \partial_i^\# E^\#
\end{aligned}$$

or

$$\begin{aligned}
(A20) \quad \frac{\partial_i x_m}{x_m} + \left[\frac{S''_m(E_m, \mathbf{v})}{S'_m(E_m, \mathbf{v})} \right] \partial_i E_m + \frac{\partial_i S'_m(., \mathbf{v})}{S'_m(E_m, \mathbf{v})} \\
- \left[\frac{C''(E, \mathbf{v})}{C'(E, \mathbf{v})} \right] \partial_i E + \left[\frac{\partial_i C'(., \mathbf{v})}{C'(E, \mathbf{v})} \right]
\end{aligned}$$

$$\begin{aligned}
(A21) \quad \frac{\partial_i x_m}{x_m} + \left[\frac{S''_m(E_m^\#, \mathbf{v}^\#)}{S'_m(E_m^\#, \mathbf{v}^\#)} \right] \partial_i E_m^\# = \left[\frac{C''(E^\#, \mathbf{v}^\#)}{C'(E^\#, \mathbf{v}^\#)} \right] \partial_i E^\#.
\end{aligned}$$

Finally, we differentiate (A4) to get

$$\begin{aligned}
(A22) \quad \partial_i N q_m S_m(E_m, \mathbf{v}) + N q_m [(S'_m(E_m, \mathbf{v}) \partial_i E_m + \partial_i S_m(., \mathbf{v}))] \\
= \sum_n \left[\left(\frac{\partial f_m}{\partial x_n} \right) \right] \partial_i x_n
\end{aligned}$$

which together with (A4) give

$$\begin{aligned}
(A23) \quad \frac{\partial_i N}{N} + \left[\frac{S'_m(E_m, \mathbf{v})}{S_m(E_m, \mathbf{v})} \partial_i E_m + \frac{\partial_i S_m(., \mathbf{v})}{S_m(E_m, \mathbf{v})} \right] = \sum_n \left[\frac{(\partial f_m / \partial x_n)}{f_m} \right] \partial_i x_n.
\end{aligned}$$

When $\mathbf{v}^\# = \mathbf{v}$

$$\begin{aligned}
 (A24) \quad & -\partial_i \Pi^\# = \partial_i (\Pi - \Pi^\#) \\
 & = EC'(E, \mathbf{v}) \left[\sum_m \frac{\sigma_m \theta_m \partial_i S_m(\cdot, \mathbf{v})}{S_m(E_m, \mathbf{v})} - \frac{\kappa \partial_i C(\cdot, \mathbf{v})}{C(E, \mathbf{v})} \right] \\
 & = \partial_i^\# \Pi^\#
 \end{aligned}$$

which is equation (4.6). Also,

$$\begin{aligned}
 (A25) \quad & p_m q_m x_m [S_m''(E_m, \mathbf{v}) \partial_i (E - E^\#) + \partial_i S_m'(\cdot, \mathbf{v})] \\
 & = [C''(E, \mathbf{v}) \partial_i (E - E^\#) + \partial_i C'(\cdot, \mathbf{v})]
 \end{aligned}$$

and comparing with marginal rule for direct ES

$$\partial_i (E_m - E_m^\#) = -\partial^\# E_m^\# \quad \text{or} \quad \partial_i (E_m - E_m^\#) = -\partial^\# (E_m - E_m^\#).$$

Evolution: Second variation.

1. *Varying the invaders phenotype.*

$$\begin{aligned}
 (A26) \quad & \partial_i^\# \partial_j^\# \Pi^\# = \sum_m p_m q_m x_m [\partial_j^\# S_m'(E^\#, \mathbf{v}^\#) \partial_i^\# E_m^\# + \partial_i^\# \partial_j^\# S_m(\cdot, \mathbf{v}^\#)] \\
 & - [\partial_j^\# C'(E^\#, \mathbf{v}^\#) \partial_i^\# E^\# + \partial_i^\# \partial_j^\# C(\cdot, \mathbf{v}^\#)] \\
 & = C'(E^\#, \mathbf{v}^\#) \sum_m \left[\left\{ \frac{\partial_j^\# S_m'(E^\#, \mathbf{v}^\#)}{S_m'(E_m^\#, \mathbf{v}^\#)} \right\} \partial_i^\# E_m^\# + \frac{\partial_i^\# \partial_j^\# S_m(\cdot, \mathbf{v}^\#)}{S_m'(E_m^\#, \mathbf{v}^\#)} \right] \\
 & - \left[\frac{\partial_j^\# C'(E^\#, \mathbf{v}^\#)}{C'(E^\#, \mathbf{v}^\#)} \right] \partial_i^\# E^\# + \frac{\partial_i^\# \partial_j^\# C(\cdot, \mathbf{v}^\#)}{C'(E^\#, \mathbf{v}^\#)} \\
 & = E^\# C'(E^\#, \mathbf{v}^\#) \left[\sum_m \sigma_m \theta_m \left\{ \frac{\partial_j^\# S_m'(E^\#, \mathbf{v}^\#)}{S_m(E_m^\#, \mathbf{v}^\#)} \right\} \partial_i^\# E_m^\# \right. \\
 & \quad \left. + \frac{\partial_i^\# \partial_j^\# S_m(\cdot, \mathbf{v}^\#)}{S_m(E_m^\#, \mathbf{v}^\#)} \right] - \kappa \frac{\partial_j^\# C'(E^\#, \mathbf{v}^\#)}{C(E^\#, \mathbf{v}^\#)} \partial_i^\# E^\# + \frac{\partial_i^\# \partial_j^\# C(\cdot, \mathbf{v}^\#)}{C(E^\#, \mathbf{v}^\#)}
 \end{aligned}$$

where $\mathbf{v}^\# = \mathbf{v}$ this becomes

$$\begin{aligned}
 (A27) \quad & \partial_i^\# \partial_j^\# \Pi^\# = C'(E, \mathbf{v}) \sum_m \left[\frac{\partial_j S_m'(E_m, \mathbf{v})}{S_m'(E_m, \mathbf{v})} \partial_i^\# E_m^\# + \frac{\partial_i \partial_j S_m(\cdot, \mathbf{v})}{S_m'(E_m, \mathbf{v})} \right. \\
 & \quad \left. - \frac{\partial_j C'(E, \mathbf{v})}{C'(E, \mathbf{v})} \partial_i^\# E^\# + \frac{\partial_i \partial_j C(\cdot, \mathbf{v})}{C'(E, \mathbf{v})} \right]
 \end{aligned}$$

varying the incumbent's phenotype

$$\begin{aligned}
 0 &\equiv \partial_i \partial_j \Pi \\
 &= \sum_m p_m q_m [\partial_i \partial_j x_m S_m(E_m, \mathbf{v}) + \partial_j x_m S'_m(E_m, \mathbf{v}) \partial_i E_m \\
 (A28) \quad &\quad + \partial_j x_m \partial_i S_m(E_m, \mathbf{v}) + \partial_i x_m \partial_j S_m(E_m, \mathbf{v}) \\
 &\quad + x_m \partial_j S'_m(\cdot, \mathbf{v}) \partial_i E_m + x_m \partial_i \partial_j S_m(\cdot, \mathbf{v}) \\
 &\quad - [\partial_j C'(E, \mathbf{v}) \partial_i E + \partial_i \partial_j C(\cdot, \mathbf{v})]]
 \end{aligned}$$

$$\begin{aligned}
 (A29) \quad \partial_i \partial_j \Pi^\# &= \sum_m p_m q_m \left[\partial_i \partial_j x_m S_m(E_m^\#, \mathbf{v}^\#) + \partial_j x_m S'_m(E_m^\#, \mathbf{v}^\#) \partial_i E_m^\# \right].
 \end{aligned}$$

Now let $\mathbf{v}^\# = \mathbf{v}$

$$\begin{aligned}
 -\partial_i \partial_j \Pi^\# &= \partial_i \partial_j (\Pi - \Pi^\#) \\
 &= \sum_m p_m q_m \partial_j x_m S'_m(E_m, \mathbf{v}) \partial_i (E_m - E_m^\#) \\
 &\quad + \left[\sum_m p_m q_m x_m \partial_j S'_m(\cdot, \mathbf{v}) \partial_i E_m - \partial_j C'(E, \mathbf{v}) \partial_i E \right] \\
 &\quad + \left[\sum_m p_m q_m x_m \partial_i \partial_j S_m(\cdot, \mathbf{v}) - \partial_i \partial_j C(\cdot, \mathbf{v}) \right] \\
 &\quad + \sum_m p_m q_m \partial_i x_m \partial_j S_m(E_m, \mathbf{v}) \\
 &\quad + \sum_m p_m q_m \partial_j x_m \partial_i S_m(E_m, \mathbf{v}) \\
 &= EC'(E, \mathbf{v}) \sum_m \sigma_m \theta_m \left\{ \frac{\partial_j x_m}{x_m} \left[\frac{S'_m(E_m, \mathbf{v})}{S_m(E_m, \mathbf{v})} \right] \partial_i E_m^* \right. \\
 &\quad \left. + \frac{\partial_i x_m}{x_m} \left[\frac{\partial_j S'_m(\cdot, \mathbf{v})}{S_m(E_m, \mathbf{v})} \right] + \frac{\partial_j x_m}{x_m} \left[\frac{\partial_i S_m(E_m, \mathbf{v})}{S_m(E_m, \mathbf{v})} \right] \right\} \\
 &\quad + EC'(E, \mathbf{v}) \left\{ \sum_m \sigma_m \theta_m \frac{\partial_j S'_m(\cdot, \mathbf{v})}{S_m(E_m, \mathbf{v})} \partial_i E_m - \kappa \frac{\partial_j C'(\cdot, \mathbf{v})}{C(E, \mathbf{v})} \partial_i E \right\} \\
 &\quad + EC'(E, \mathbf{v}) \left\{ \sum_m \sigma_m \theta_m \partial_i \partial_j \frac{S_m(\cdot, \mathbf{v})}{S_m(E_m, \mathbf{v})} - \kappa \frac{\partial_i \partial_j C(\cdot, \mathbf{v})}{C(E, \mathbf{v})} \right\}
 \end{aligned}$$

which is equation (4.13). Note that $\partial_i(E_m - E_m^\#)$ can be recovered from

$$\frac{S_m''(E_m, \mathbf{v})}{S'(E_m, \mathbf{v})} \partial_j^\# E_m^\# + \frac{\partial_j S_m'(\cdot, \mathbf{v})}{S'(E_m, \mathbf{v})} = \frac{C''(E, \mathbf{v})}{C'(E, \mathbf{v})} \partial_j^\# E^\# + \frac{\partial_j C'(\cdot, \mathbf{v})}{C'(E, \mathbf{v})}$$

but that $\partial_i E_m$ must be obtained simultaneously with $\partial_i x_m$ using both (A18), (A19) and (A20), (A21).

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DEPARTMENT OF MATHEMATICAL SCIENCES, UNIVERSITY OF MONTANA, MISSOULA, MT 59812