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Evaluation of Phase Integrals for Volterra Systems of Arbitrary Numbers of Interacting Species

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A general method is presented for the evaluation of phase integrals of the Volterra model of stable predator–prey interactions for any fixed number $N \geqslant 2$ of interacting species. The method is based on a bijective transformation of trajectory surfaces onto a flat hyperplane in Euclidean N-space, parametrized by a new set of dynamical variables in terms of which integration over the surface is straightforward. Expressions are displayed for the surface area of the trajectory surface and for the volume contained within this surface, quantities which are known to play an important role in the description of the statistical properties of Volterra trajectories.

KEY WORDS: Volterra system; N interacting species; evaluation of phase integrals; coordinate transformation.

1. INTRODUCTION

This is the first in a series of papers dealing with properties of the model for interacting predator–prey systems in nature defined by Volterra's equations. These systems are striking in the extent to which results of the formalism of statistical physics carry over directly to problems of population dynamics.[1–4] Because they define for populations quantities analogous to the Hamiltonian energy, the temperature, and the entropy, i.e., cardinal quantities in the characterization of the macroscopic behavior of physical systems, these results suggest potentially powerful new methods for the study of populations. The present series is concerned with the application of such methods to obtain direct experimental tests of the Volterra model, as well as to indicate ways of deriving from it laws of population behavior which probably transcend the dynamics of the model itself.

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We sketch the analogy between a Volterra system and a classical mechanical system. Volterra's equations are a system of N first-order nonlinear differential equations expressing the time rate of change of the population numbers of the N individual interacting species. They represent the equations of motion. Volterra[7] himself discovered in integral of the system, analogous to the Hamiltonian. It is the work of Kerner which initiated the present direction of research. He demonstrated, first, that one could transform Volterra's equations such that the induced dynamical flow was measure-preserving on the new phase space, in analogy to Liouville's theorem. Assuming the ergodic hypothesis, he then replaced time averages with phase averages with respect to the microcanonical density and obtained important results about the moments of the distribution of population numbers with standard methods of the microcanonical formalism. Finally, he pointed out that for systems of many interacting species, the Volterra integral partitions into small and large components in the manner required to apply the transition from microcanonical to canonical systems developed by Khintchine.[5] He then applied canonical formalism to calculate time averages of functions of individual species numbers in the population. Recently, Goel *et al.*[1] made a fundamental contribution to this program in providing a systematic means of analysis of Volterra's equations to determine whether a given population is stable or whether it tends in time to the extinction of some of its species.

The task of the present paper is to obtain a form of the phase integrals of Volterra systems of N interacting species, for arbitrary N, in which they can be readily evaluated. Need for solution of this problem arises directly in attempts to compare the predicted behavior of Volterra systems with populations in nature. Volterra's equations contain $N(N + 3)/2$ independent parameters. Although in principle these parameters can be expressed in terms of quantities estimated from population data by means of the methods of statistical mechanics, such methods introduce phase integrals not soluble by quadratures which effectively block application of the expressions. In the following paper, we shall use the results found here to obtain soluble expressions for the five model parameters of the two-species model. These expressions provide direct tests of the Volterra model for the two-species case. The main utility of these solutions probably lies beyond the testing of the Volterra model itself, however. At the present level of understanding of population dynamics, there is nothing known which corresponds to either the laws of thermodynamics or phase functions useful in characterizing population behavior. We expect that the appropriate role of the Volterra model is that of any such population model, i.e., that it suggest which functions ought to be studied for the purpose of writing general laws of population behavior. For example, the quantities formally equivalent to the temperature and entropy of physical systems, which appear in the expressions for the parameters of the two-species case, are phase integrals. The capacity to evaluate such integrals is essential to this approach.

2. ANALYSIS

The Volterra equations for N interacting species,[6]

$$dN_i/dt = k_i N_i + \beta_1^{-1} \sum_{j=1}^{N} \alpha'_{ij} N_i N_j, \qquad i = 1,\ldots, N \tag{1}$$

$$\alpha'_{ij} = -\alpha'_{ji}, \qquad i, j = 1,\ldots, N$$

state the time rate of change of the numbers N_i of organisms of the ith species in terms of: (a) rate constants k_i, positive for prey and negative for predator, characterizing the (exponential) growth or decline of the individual species in isolation, (b) an $N \times N$ interaction matrix (α'_{ij}) subtracting an interaction term from the growth rates of prey and adding to those of predators; and (c) scaling constants β_i, measuring, heuristically, the numbers of prey lost for gains in single predators, so chosen that by definition the matrix (α'_{ij}) is completely antisymmetric. For convenience, we absorb the scaling constant by the transformations

$$x_i = \beta_i N_i, \qquad \alpha_{ij} = (\beta_i \beta_j)^{-1} \alpha'_{ij}$$

and write the Volterra equations as

$$dx_i/dt = k_i x_i + \sum_{j=1}^{N} \alpha_{ij} x_i x_j, \qquad i = 1,\ldots, N \tag{2}$$

$$\alpha_{ij} = -\alpha_{ji}, \qquad i, j = 1,\ldots, N$$

We consider only solutions in which no species goes to extinction in the process of time evolution, i.e., cases in which the dynamical variables x_i are bounded away from zero from below. With this assumption, a necessary and sufficient condition for the existence of fixed points of Volterra's equations is clearly

$$k_i + \sum_{j=1}^{N} \alpha_{ij} x_j = 0, \qquad i = 1,\ldots, N \tag{3}$$

Let any solution $\mathbf{x}$ of this condition be denoted by the vector $\mathbf{q}$. Then systems with the initial conditions $x_i = q_i$ for all species are static throughout time.

If a system admits a fixed point, another transformation of Volterra's equations is useful. Define $y_i = x_i - q_i$. Then

$$dy_i/dt = \sum_{j=1}^{N} \alpha_{ij} x_i y_j = dx_i/dt, \qquad i = 1,..., N \tag{4}$$

Existence of a fixed point leads directly to an integral of Volterra's equations.[7] In fact, define $G = G(\mathbf{x})$ by

$$G = \sum_{i=1}^{N} q_i \left(\frac{x_i}{q_i} - \log \frac{x_i}{q_i} - 1 \right) \tag{5}$$

Then

$$\frac{dG}{dt} = \sum_{i=1}^{N} \frac{y_i}{x_i} \frac{dx_i}{dt} = \sum_{i,j=1}^{N} \alpha_{ij} x_i x_j = 0$$

the final equality following from the antisymmetry of the matrix (α_{ij}). We mention that the function G defined here differs from that usually given in the literature by the constant $\sum_{i=1}^{N} q_i$. The function G will play the role of the Hamiltonian in the formalism.

Application of the methods of statistical mechanics in calculation of the long-time averages of phase functions requires that the Volterra system satisfy the ergodic hypothesis. To this purpose, Kerner[3] introduced a new set of dynamical variables $v_i = \log(x_i/q_i)$, $i = 1,..., N$. The transformation $\mathbf{x} \mapsto \mathbf{v}$ is one-to-one onto its range because of the monotonicity of the log function. Note that, since Volterra's equations are a system of N first-order equations, their solutions may be represented as trajectories in a Cartesian N-space with either $\mathbf{x}$ or $\mathbf{v}$ as coordinates. We denote by X this $\mathbf{v}$-space, which is suitable for ergodic theory. Kerner then showed that the Volterra transformation is (Lebesgue) measure-preserving on X. If, moreover, the system is metrically transitive on surfaces of constant G, then the ergodic hypothesis is satisfied, and to within a set of initial phases of measure zero one may equate, using the results of Khintchine,[5]

$$\langle f \rangle_t \overset{\text{def}}{=} \lim_{t \to \infty} t^{-1} \int_0^t f\, dt = \Omega^{-1} \int_{[G=g]} \frac{f}{|\nabla G|}\, dS \overset{\text{def}}{=} \langle f \rangle \tag{6}$$

for any absolutely integrable (L_1) function f. Here, the function $\Omega = \Omega(G)$ is the normalization to unity. With respect to this assumption, Goel *et al.*[1] demonstrated that the linear approximation of the Volterra system is ergodic in the limit of large N. We shall show in the following paper that the 2-species (nonlinear) Volterra system is rigorously ergodic. For arbitrary N, we shall assume the ergodic hypothesis to obtain.

Expressions for the mean and mean-square oscillations of a Volterra system of arbitrary N, found by replacing the time average with the phase average as in Eq. (6), have already been given in the literature. We display these calculations here because they illustrate the central problem in the Volterra analysis which has led to the task of the present paper. For the mean, note, then, that

$$\langle y_i \rangle = \frac{1}{\Omega(g)} \int_{[G=g]} \frac{y_i}{|\nabla G|} \, dS = \frac{1}{\Omega(g)} \sum_{j=1}^{N} \int_{[G=g]} \delta_{ij} \, dS_j$$
$$= \frac{1}{\Omega(g)} \sum_{j=1}^{N} \int_{[G=g]} \frac{\partial}{\partial v_j} (\delta_{ij}) \, d\mathbf{v} = 0 \tag{7}$$

where dS_i is the ith component of the surface element of the closed surface $[G = g]$. We observe that $\partial G/\partial v_i = y_i$. But if $\langle y_i \rangle = \langle x_i - q_i \rangle = 0$, then $\langle x_i \rangle = q_i$. This result is due to Kerner.(3) The intensity or mean square oscillation is

$$\langle y_i^2 \rangle = \frac{1}{\Omega(g)} \int_{[G=g]} \frac{y_i^2}{|\nabla G|} \, dS = \frac{1}{\Omega(g)} \sum_{j=1}^{N} \int_{[G=g]} y_i \, \delta_{ij} \, dS_j = \frac{1}{\Omega(g)} \int_{[G=g]} x_i \, d\mathbf{v}$$

This integral may be evaluated by means of the fact that

$$\int_{[G=g]} \frac{1}{|\nabla G|} \, dS = \frac{d}{dg} \int_{[G=g]} f \, d\mathbf{v} \tag{8}$$

for any L_1 function f, a result due to Khintchine(5) which we shall use in a critical way below. In the present instance,

$$\frac{d}{dg} \int_{[G=g]} x_i \, d\mathbf{v} = \int_{[G=g]} \frac{x_i}{|\nabla G|} \, dS = q_i \Omega(g)$$

Hence,

$$\frac{1}{\Omega(g)} \int_{[G=g]} x_i \, d\mathbf{v} = \frac{q_i}{\Omega(g)} \int_{[G=g]} \Omega(g) \, dG = \frac{q_i}{\Omega(g)} \int_{[G=g]} d\mathbf{v}$$

Denoting the integral over the volume enclosed by the constant-G surface by W,

$$W(g) = \int_{[G=g]} d\mathbf{v}$$

we obtain finally

$$\langle y_i^2 \rangle = q_i W(g)/\Omega(g) \tag{9}$$

This result, obtained in a different way, is given by Goel *et al.*(1)

These results, derived by use of Gauss' theorem and the relationship between y_i and the gradient of the function G, are a standard calculation in classical statistical mechanics. For the mean, they carry through to a numerical result. However, for any higher moment, including the mean square, they introduce integrals such as W and Ω which cannot be evaluated without explicit parametrization of the trajectory $[G = g]$ in terms of the arc length.

The major analytical task in the following, to which we now turn, will be to obtain this parametrization. For the sake of conceptualization of the approach, we shall divide analysis into the cases $N = 2$ and $N > 2$, solving the former completely before proceeding to the general case. This division has the further utility that it is the two-species case alone that is the subject of the following paper.

Define, then, the transformation $\xi_i = q_i(e^{v_i} - v_i - 1)$, $i = 1, 2$, and denote by Y the Cartesian 2-space with coordinates (ξ_1, ξ_2). In terms of the new coordinates, the invariance condition on G becomes $G = \xi_1 + \xi_2$, identifying G as just the scalar invariant of the vectors (ξ_1, ξ_2) and $(1, 1)$ in Y. Hence, the set $[G = g]$, for any $g > 0$, is the straight line in Y of slope (-1) with intercepts $(0, g)$ and $(g, 0)$, respectively. In order to trace the Volterra trajectory along the line $\xi_2 = g - \xi_1$, we elaborate the major properties of the transformation $\mathbf{v} \mapsto \boldsymbol{\xi}$. Observe, first, that the trajectory in X is an analytic closed curve about the origin. In fact, the rate of change of the slope in X is

$$(d/dt)(dv_2/dv_1) = -(d/dt)(y_1/y_2) = -(\alpha_{12}/y_2^2)(x_2y_1^2 + x_1y_2^2) \quad (10)$$

Since the x_i are bounded away from zero below by hypothesis, the right-hand side always has a sign opposite to that of α_{12}. If we arbitrarily take species 1 as predator, once and for all, then $\alpha_{12} > 0$. With this convention, the rate of change in slope then exists and is nonpositive throughout the motion. Since $G = 0$ at the point (0, 0), the origin cannot lie on any trajectory for $G > 0$. The conclusion then follows from the fact that in each quadrant of X, to any value of $G > 0$ there corresponds at most one value of v_1 (resp., v_2) for any fixed value of v_2 (v_1), as we now show. Indeed, we obtain the more general fact that the mapping $\mathbf{v} \mapsto \boldsymbol{\xi}$ on each of the four quadrants of X is one-to-one onto the closed triangular area defined by the coordinate axes and the line $[G = g]$ in Y. Note, first, that since $d\xi_i/dv_i = q_i(e^{v_i} - 1) = y_i$ and $d^2\xi_i/dv^2 = q_ie^{v_i} = x_i > 0$, the graph of ξ_i against v_i has a single minimum, zero, at $x_i = q_i$, and is everywhere convex downward. Hence only nonnegative values of ξ_i correspond to real roots v_i. Moreover, to each positive value of ξ_i there correspond exactly two roots v_i, one positive and one negative. We denote these roots by v_i^+ and v_i^-, respectively. The value $\xi_i = 0$ has the single root $v_i = 0$. The absolute values of both roots $v_i^\pm$ increase monotonically with increasing ξ_i. This assures in the above that the trajectory is closed in X. Now fix any $g > 0$. Since $\xi_2 = G - \xi_1$, $\xi_2' < \xi_2$ for any $g' < g$, and therefore $|v_2{}^\pm| < |v_2{}^\pm|$ for all fixed $v_1{}^+$ or $v_1{}^-$, and similarly $|v_1'^\pm| < |v_1{}^\pm|$ for all fixed $v_2{}^+$ or $v_2{}^-$. It follows on inspection that the trajectory $[G = g']$ is completely contained within the trajectory $[G = g]$ in X. Obviously the triangle formed with the coordinate axes by the hypotenuse $[G = g']$ is contained within that of the hypotenuse $[G = g]$ in the first quadrant of Y. Now, each point in the first quadrant of Y lies on a unique line of the form

$[G = g]$, for some g, i.e., on a unique trajectory, and conversely each point in X lies on a unique trajectory. The mapping $\mathbf{v} \mapsto \boldsymbol{\xi}$ is therefore onto. Moreover, since $(v_1'^+, v_2'^+) \neq (v_1{}^+, v_2{}^+)$ implies that $\boldsymbol{\xi}' \neq \boldsymbol{\xi}$, the mapping on the first quadrant of X is one-to-one onto Y. The same conclusion applies to each of the other quadrants by change of sign choice. This completes the proof of bijection. Finally, it follows immediately from the preceding that the area contained within the trajectory $[G = g]$ in each quadrant of X maps onto that within the triangle with hypotenuse $[G = g]$ in the first quadrant of Y.

We have found that the phase point in X moves continuously in a closed trajectory about origin, in fact, in a clockwise direction with the above species designation. Transforming this result, we now find that the phase point initially at $(g, 0)$, say, in Y moves up the line $\xi_2 = g - \xi_1$ to $(0, g)$, then back to its starting point, then up and back again, for each single passage about the trajectory in X. From Eq. (10) and the proved inclusions, we also obtain the fact, important in ergodic theory, that the area contained within the trajectory $G = g$ in X is a simply connected, convex body. That is, if any two points both lie inside the trajectory, then all points on the straight line connecting them also lie within the trajectory. The same fact is clearly true of the triangles defined by trajectories in Y. Moreover, the area (Lebesgue measure) contained within the trajectory, in either space, is a monotone increasing function of G.

Having transformed trajectories into straight lines with the mapping $\mathbf{v} \mapsto \boldsymbol{\xi}$, whatever their shape in X and for any value of G, we can now write on inspection an additional transformation to a coordinate system which completes the parametrization of the trajectory. Indeed, fix any point (ξ_1, ξ_2) in the first quadrant of Y, and construct the straight line of slope (-1) that passes through this point. Let r be the perpendicular distance of this line from the origin, and let z be the length along this line from its ξ_2 intercept to the given point (ξ_1, ξ_2). The transformations defined in this way are $\xi_1 = 2^{-1/2}z$ and $\xi_2 = 2^{-1/2}(2^{1/2}r - z)$. We observe that a point (r, z) lies on the trajectory $[G = g]$ if, and only if, $r = 2^{-1/2}g$. Moreover, one sweeps the entire area $[G \leqslant g]$ exactly once in each of the four quadrants by allowing z to vary from 0 to $2^{1/2}r$, and r from 0 to $2^{-1/2}g$, holding to a particular sign choice of the roots (v_1, v_2), and in all four quadrants by a fourfold integration, once for each choice of paired signs.

We write the general phase integral in terms of the coordinates (z, r). For the right side of Eq. (8), we have

$$\frac{d}{dg}\int_{[G \leqq g]} f(v_1, v_2)\, dv_1\, dv_2 = \frac{d}{dg}\int_0^g dr \int_0^{2^{1/2}r} f(g, z)\, \frac{\partial(v_1{}^\pm, v_2{}^\pm)}{\partial(r, z)}\, dz$$

$$= \int_0^{2^{1/2}g} f(g, z)\, \frac{\partial(v_1{}^\pm, v_2{}^\pm)}{\partial(r, z)}\, dz \qquad (11)$$

where $\partial(v_1{}^{\pm}, v_2{}^{\pm})/\partial(z, r) = (y_1 y_2)^{-1}$ is the Jacobian of the transformation $v \mapsto (z, r)$, and where the notation indicates, in an obvious way, the required fourfold integration just described. We note, for future reference, that the Jacobian of the transformation $\xi \mapsto (z, r)$ is one. The expectation value of a phase function f becomes

$$\langle f \rangle = \frac{1}{\Omega}\int_0^{2^{1/2}G} \frac{f(G, z)}{y_1{}^{\pm} y_2{}^{\pm}}\, dz$$
$$= \frac{2^{1/2}}{\Omega}\int_0^{G} \left[\frac{f(y_1{}^{+}, y_2{}^{+})}{y_1{}^{+} y_2{}^{+}} - \frac{f(y_1{}^{+}, y_2{}^{-})}{y_1{}^{+} y_2{}^{-}} + \frac{f(y_1{}^{-}, y_2{}^{-})}{y_1{}^{-} y_2{}^{-}} - \frac{f(y_1{}^{-}, y_2{}^{+})}{y_1{}^{-} y_2{}^{+}}\, d\xi_1\right] \tag{12}$$

In the very important case of the normalization constant $\Omega = \langle 1 \rangle$, we write Eq. (10) in a different form to avoid improper integrals. Noting that $dz = 2^{1/2}\, d\xi_1 = -2^{1/2}\, d\xi_2$ and $d\xi_i = y_i\, dv_i = x_i^{-1}(x_j - q_j)\, dx_i$ $(i, j = 1, 2;\ i \neq j)$, we find

$$2^{-1/2}\int_0^{2^{1/2}G} \frac{1}{y_1 y_2}\, dz = \int_0^{G/2} \frac{1}{y_1 y_2}\, d\xi_1 + \int_0^{G/2} \frac{1}{y_1 y_2}\, d\xi_2$$
$$= \int_0^{\xi_1 = G/2} \frac{1}{x_1(x_2 - q_2)}\, dx_1 + \int_0^{\xi_2 = G/2} \frac{1}{x_2(x_1 - q_1)}\, dx_2 \tag{13}$$

for any sign choice. Since x_i approaches q_i only as ξ_j approaches G, $i \neq j$, both integrals on the right are proper. The full integration for Ω is just the sum over four such pairs, corresponding to the four choices of paired signs.

Since we cannot simply invert $y_i = q_i(e^{v_i} - 1)$, these integrals are still not soluble by quadratures. They are, however, in a form which readily admits numerical evaluation. Equation (10) thus completes the task of this paper for the case $N = 2$.

We now treat the N-species case, for arbitrary N, by straightforward extension of the analysis for two species. Since the discussion of coordinate transformations is necessarily complicated, let us relate it to a common problem in multiple integration with which it is directly analogous. It is desired to calculate surface and volume integrals in $\mathbf{v}$-space on the domain contained within the surface $[G = g]$. We suspect, and shall demonstrate, that the domain is a convex body, but its shape is an unseemly "lopsided egg" (see the figures in Ref. 1) if $N = 2$ and is unknown altogether if $N > 2$. The problem is nevertheless analogous to the calculation of surface and volume integrals on a sphere about the origin in 3-space. This is a difficult problem in rectangular coordinates because the equation describing the spherical surface mixes the coordinates of integration in such a way that the limits of integration in one variable depend on the other variables. It is a simple calculation in spherical polar coordinates because here the radial vector, varying over known limits, fills the sphere with disjoint spherical shells, while the angular variables, for any fixed value of r, parametrize the spherical shell corresponding to that value of r and sweep, for known limits, independent of r, that entire shell. In the following, we accomplish the same thing for the Volterra surface $[G = g]$. First, we transform into a coordinate system in which the surface $[G = g]$ is necessarily a flat hyperplane of known orientation in N-space. The volume contained within the surface in $\mathbf{v}$-space transforms to the volume of the first quadrant of the range space contained within the hyperplane. The problem at this point is analogous to that of the sphere in rectangular coordinates, i.e., integration within a surface of known shape but with respect to a coordinate system which does not conveniently describe the surface. We then transform to a second coordinate system in which $N - 1$ coordinates parametrize the hypersurface, while the Nth coordinate translates the hypersurface throughout the volume over which integration is to be performed. Thus, the $N - 1$ coordinates correspond to the angular coordinates in the integration of the sphere, and the remaining coordinate to the radius.

As in the two-species case, define now the coordinates $\xi_i = q_i(e^{v_i} - v_i - 1)$, $i = 1,..., N$. The set of all points $(\xi_1,..., \xi_N)$ in the Cartesian N-space, Y, say, with axes $\xi_1,..., \xi_N$ that satisfy the condition $G = \sum_{i=1}^{N} \xi_i = g$ is a plane orthogonal to the vector $(1,..., 1)$. Fix any point P in the first quadrant of this space. Let r be the perpendicular distance, in the Euclidean metric of the space, from the origin to the plane parallel to $[G = g]$ that passes through P. Construct the planes of the form $\xi_i = \text{const}$, $i = 1,..., N - 1$, which contain P, and let z_i be the length of the line segment from the axis ξ_N to the ith such plane along the intersection of the $\xi_i - \xi_N$ coordinate plane and the plane $[G = g]$. The transformations for the z_i are $z_i = 2^{1/2}\xi_i$, $i = 1,..., N - 1$. The transformation for r is $r = (\sum_{i=1}^{N} \xi_i) \sin \vartheta$, where ϑ is the angle formed by the vector $(1,..., 1)$ with the coordinate plane $\xi_N = 0$. To find $\sin \vartheta$, we denote by $\mathbf{r} = (a,..., a)$ the vector normal from the origin to the plane $[G = g]$. The components a, which are identical for all N coordinates by symmetry, are to be determined. Now $\xi_i = (a,..., a)(0,..., 1,..., 0) = a$, $i = 1,..., N$. Since the point $(a,..., a)$ lies in the plane $[G = g]$, the vector $\boldsymbol{\xi}$ with components $\xi_i = a$ must satisfy the defining condition of the plane, i.e., $\sum_{i=1}^{N} \xi_i = Na = g$. Then $r = (\sum_{i=1}^{N} a^2)^{1/2} = N^{-1/2}g$. It follows from simple geometry that $\sin \vartheta = r/g = N^{-1/2}$. Hence, the transformation from $\boldsymbol{\xi}$ to r is $r = N^{-1/2} \sum_{i=1}^{N} \xi_i$.

The coordinate $(z_1,..., z_{N-1}, r) = (\mathbf{z}, r)$, for any r, are a suitable parametrization of the states of the N-species Volterra system. Indeed, the proof that the mapping $\mathbf{v} \mapsto (\mathbf{z}, r)$ from each quadrant of X onto the first quadrant of Y is one-to-one is exactly analogous to that for the two-species case. Conversely, each point in the first quadrant of Y corresponds to $2N$ points in X, one for each choice of signs of the two roots of the N equations $\xi_i = q_i(e^{v_i} - v_i - 1)$.

The Jacobian of the transformation $\mathbf{v} \mapsto \boldsymbol{\xi}$, with elements $\partial v_i/\partial \xi_j = y_i^{-1}\,\delta_{ij}$, is diagonal with value $(y_1 \cdots y_N)^{-1}$. The transformation $\boldsymbol{\xi} \mapsto (\mathbf{z}, r)$ has Jacobian with elements $\partial \xi_i/\partial z_j = 2^{-1/2}\,\delta_{ij}$, $i, j = 1,\ldots, N-1$, and $\partial \xi_i/\partial r = N^{1/2}\,\delta_{iN}$, $i = 1,\ldots, N$, which is diagonal with value $(N/2^{N-1})^{1/2}$. The Jacobian of the full transformation $\mathbf{v} \mapsto (\mathbf{z}, r)$ is the product of the two, with value $(N/2^{N-1})^{1/2}(y_1 \cdots y_n)^{-1}$.

The phase average of an arbitrary L_1 function of a Volterra system of N species is therefore

$$\langle f\rangle = (N/2^{N-2})^{1/2} \int_0^G \frac{d\xi_1}{y_1^{\pm}} \cdots \int_0^G \frac{d\xi_{N-2}}{y_{N-2}^{\pm}} \int_0^G \frac{f}{y_{N-1}^{\pm} y_N^{\pm}}\, d\xi_{N-1} \tag{14}$$

where the notation indicates a sum over 2^N integrals of the form on the right, one for each choice of signs, each integral weighted by $+1$ if the number of negative roots is even and -1 if the number is odd. If f is a linear combination of products of powers $y_1^{n_1} \cdots y_N^{n_N}$, then Eq. (12) assumes the simple form

$$\langle f\rangle = (N/2^{N-2})^{1/2} \int_0^G [(y_1^{+})^{n_1-1} - (y_1^{-})^{n_1-1}] \cdots [(y_N^{+})^{n_N-1} - (y_N^{-})^{n_N-1}]\, d\xi_1 \cdots d\xi_{N-1} \tag{15}$$

The proof of convergence for the case $n_i = 0$, $i = 1,\ldots, N$, is directly analogous to that for the two-species case. We note that any continuous function f on Y may be approximated, with arbitrary precision, by a linear combination of this form (Stone–Weierstrass theorem). This completes the task of the present paper.

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