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On ‘Fisher Zero’ coevolutionary singularities in the Extended Evolutionary Synthesis

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Abstract

We outline a ‘mathematically elegant’ formulation of the Extended Evolutionary Synthesis that embeds genetic heritage within a more comprehensive structure including environment, development, niche construction, and large deviations, all under the influence of a stochastic burden that sculpts evolutionary response. The work is based on the asymptotic limit theorems of information theory, modulo abduction of appropriate methodology from statistical mechanics and nonequilibrium thermodynamics. The formalism could rejuvenate interplay between model-based evolutionary predictions and data-based observations, given that models must always remain the subordinate partner, and might further serve as a foundation for new statistical tools useful in the study of experimental and observational data.

Keywords: groupoid, information theory, phase transition, punctuated equilibrium, stochastic stability, symmetry breaking

Models are certainly not useless... [b]ut too much should not be expected of them. Modeling is only a part, and a subordinate part, of ecological research.

— E.C. Pielou (1981)

DOWN THE RABBIT HOLE

— Alice in Wonderland, Ch. 1.

1. Introduction

The famous manifesto of Laland et al. (2014) frames the central problem of contemporary evolutionary theory in these terms:

...[M]ainstream evolutionary theory has come to focus almost exclusively on genetic inheritance and processes that change gene frequencies... An alternative vision of evolution is beginning to crystallize, in which the processes by which organisms grow and develop are recognized as causes of evolution...

[O]rganisms are constructed in development, not simply ‘programmed’ to develop by genes. Living things do not evolve to fit into pre-existing environments, but co-construct and coevolve with their environments, in the process changing the structure of ecosystems...

...[A] ‘gene-centric’ focus fails to capture the full gamut of processes that direct evolution. Missing pieces include how physical development influences the generation of variation (developmental bias); how the environment directly shapes organisms; traits (plasticity); how organisms modify environments (niche construction); and how organisms transmit more than genes across generations (extra-genetic inheritance)...

Similar, more detailed, analyses abound (e.g., Laland et al., 1999, 2015; Muller 2017; Oddling-Smee et al. 2003).

From a cynical research funding stream and marketing perspective, however, a singular ‘failure’ of this Extended Evolutionary Synthesis (EES) has been the lack of a sufficiently elegant and comprehensive mathematical formulation matching that gracing (or, more to the point, fatally burdening) the innumerable gene frequency treatments of evolutionary dynamics. What might be criticized as piecemeal treatments do indeed abound (e.g., EES 2020), but the sense of ‘something big’ still seems missing.

Indeed, a central benefit of the gene frequency-centered mathematical models is that, over the decades, they have become a well-proven lucrative rabbit hole for institutional fundraising and resulting career advancement.

It can be seriously argued that a single unitary and comprehensive ‘something big’ may not actually exist for the almost infinite varieties of evolutionary process active at and across the full range of scales of biological, social, and cultural phenomena. The somewhat ludicrous demise of ‘meme theory’ for understanding social dynamics should have been a red flag that narrow gene-centered models of evolutionary process have in-

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deed become amber inclusions (Chvaja 2020).

‘Big’ aside for the moment, we will argue here that it may be possible to construct something modestly comprehensive that encompasses enough of EES to be of intellectual interest.

A number of distinctly off-brand products – R. and R.G. Wallace (1998, 1999), Wallace (2002, 2009, 2010, 2011a, b, c, 2012a, b, 2013a, b, c, 2016a), R. and D. Wallace (1998, 2008, 2009, 2011, 2016), Wallace et al. (2009), Glazebrook and Wallace (2012), R.G. and R. Wallace (2009) – outline a possible ‘big enough’ approach to the EES. The essence lies in first recognizing that the living state is cognitive, in a formal sense, at all scales and levels of organization (e.g., Maturana and Varela 1980), and in the characterization of such cognition through ‘dual’ information sources constrained by the asymptotic limit theorems of information theory (Dretske 1994; Atlan and Cohen 1998; Wallace 2012).

The rest is surprisingly straightforward – embedding ecosystems, niches, genetic, chemical epigenetic, and cultural, heritage transmission, and ‘large deviations’ can also be viewed in terms of information sources. Interaction between them occurs through an appropriate joint information source, and dynamics emerge via abduction of approximate methods from statistical mechanics and nonequilibrium thermodynamics. The lack of microreversibility inherent to information transmission – directed homotopy – leads to highly punctuated groupoid-based symmetry-breaking phase transition analogs.

We outline a moderately comprehensive theory of EES that follows from these perspectives in nine basic equations and a few examples.

2. First notions

General information sources

The essential character of an information source (Khinchin 1957; Cover and Thomas 2006) is the ability to divide streams of output into two sets, a small one of high probability, containing a relatively few ‘meaningful’ statements consonant with an underlying grammar and syntax (in a large sense), and a much larger ‘nonsense’ set of vanishingly small probability. This is the fundamental content of the Shannon-McMillan Theorem.

Underlying grammar and syntax are inherent to meaningful sequences associated with an information source.

For a stationary, ‘ergodic’ system in which cross-sectional probabilities match longitudinal probabilities, it is further possible to define a system-wide source uncertainty for an information source X as

$$H[X] = \lim_{n \rightarrow \infty} \frac{\log[N(n)]}{n} \quad (1)$$

where $N(n)$ is the number of ‘meaningful sequences’ of length n . This value is the same across all possible output sequences $x^n = \{x_0, x_1, \dots, x_n, \dots\}$, $n \rightarrow \infty$ and can be expressed in terms of ‘Shannon entropies’ having the form $-\sum_j P_j \log(P_j)$, where the P_j constitute an appropriate probability distribution.

For a stationary, non-ergodic system, however, each limiting path x^n , as $n \rightarrow \infty$ will have its own path-dependent H -value (Khinchin, 1957), not expressible as a Shannon entropy across a probability distribution.

While it is, in theory, possible to represent any non-ergodic information source as an appropriate sum or integral of ergodic sources, in our context, this would be like making a Ptolemaic epicycle expansion of Keplerian orbits. Here, via the nonequilibrium thermodynamics formalism, we will impose something of a Keplerian simplicity on non-ergodic information sources.

Biological information sources

I. Natural ecosystem observations indeed have grammar and syntax. Night follows day. Much off the Equator, seasonal variations follow predictable patterns regarding insolation, temperature, rain/snow, and the like. Within a limited ecosystem, on a limited time scale, there are expected flora and fauna that interact (roughly) in familiar patterns – mutualism, predation, symbiosis, and so forth. Call this information source Y . As an extension of theory, Y itself might well be broken into interacting niche substructure information sources.

II. Genetic heritage can be treated as information transmission. See Ademi et al. (2000), Ofria et al. (2003), Ademi and Cerf (2000) for detailed arguments. Indeed, the transmission of genetic information is much a contextual matter involving an information source that must interact with a broad spectrum of embedding ecosystem information sources. Wallace and Wallace (2009, Ch.1) provide a fuller exposition.

III. Gene expression is itself a cognitive phenomenon involving a dual information source. As Wallace (2010) puts it, a cognitive paradigm is needed to understand gene expression, much as Atlan and Cohen (1998) invoke a cognitive paradigm for the immune system. Cohen and Harel (2007) assert that gene expression is a reactive system that calls our attention to its emergent properties, i.e., behaviors that, taken as a whole, are not expressed by any one of the lower scale components that comprise it. Cellular processes react to both internal and external signals to produce diverse tissues internally, and diverse general phenotypes across various scales of space, time, and population, all from a single set or relatively narrow distribution of genes. The essence of the Atlan/Cohen cognitive paradigm is that cognition involves choice of a smaller set of actions from a much larger set available to the cognitive entity. Choice reduces uncertainty, and reduction in uncertainty implies the existence of an information source ‘dual’ to the cognitive process. The argument is direct, compelling, and intuitive.

IV. Cognitive processes on inherently unstable dynamic ‘roadways’ are almost always paired with regulatory information sources: blood pressure must not become excessive, immune systems must not attack self-tissues, consciousness in higher animals must often be paired with internalized social control, cancerous cells must be constrained, and so on. If X_i is an information source within an organism, we can expect a parallel regulatory source as X^i .

V. Large deviations (Champagnat et al. 2006; Dembo and Zeitouni 1998) follow high probability developmental pathways

governed by entropy-like laws that imply the existence of another information source, say L_D .

VI. For individual and associated collections of species, ‘selection pressures’ are not always random, but are usually highly structured so that sequences of evolutionary challenge can be associated with an information source S_P , again allowing identification ‘meaningful’ sequences according to underlying grammar and syntax.

Coevolutionary stochastic burden

Dieckmann and Law (1996) argue at some length that the study of what they call ‘asymptotic stationary states’ or ‘fixed points’ – quasi-stable conditions in evolutionary process – requires address of four critical matters:

I. The evolutionary process needs to be considered in a co-evolutionary context.

II. A proper mathematical theory of evolution should be dynamical.

III. The coevolutionary dynamics ought to be underpinned by a microscopic theory.

IV. The evolutionary process has important stochastic elements.

We will, in fact, recover something like the Dieckmann and Law (1996) perspective in Eq.(9) below, but without using the canonical equation of evolutionary game dynamics.

In what follows, then, we attempt to span these two sets of points in a comprehensive ‘mathematically elegant’ manner. Other approaches, of course, might well be taken e.g., Gonzalez-Forero and Gardner (2021, 2022), who extend the evolutionary game dynamics results.

3. The theory

Ecosystem-embedded coevolutionary process, as we have characterized it here, can thus be described by a joint information source having an uncertainty (Cover and Thomas 2006):

$$H(\{X_i, X^i\}, Y, L_D, S_P) \quad (2)$$

This source is unlikely to be ergodic and thus cannot be characterized as Shannon entropies across some appropriate probability distribution. That is, each joint path converges to an individual source uncertainty value as sequence length increases. See Khinchin (1957) for a detailed discussion. For nonergodic information sources, as described above, it remains possible to assign a path dependent information source uncertainty to each possible – sufficiently long – high-probability path.

The set $\{X_i, X^i\}$ is taken to pair the basic cognitive biological process X_i with a regulatory process X^i : for biological systems, major cognitive phenomena are almost always paired with essential regulators, as in gene expression and immune function across the life course. Indeed, progressive failure of such bioregulators in higher animals most often drives diseases of aging.

We now construct an index of the rate at which essential resources can be delivered to elements within the coevolutionary ecosystem of interest. This involves scalarization of a possible

multidimensional set of resources including the basic metabolic free energy sources, ecosystem richness in terms of predation, mutualism, symbiosis, and the like.

In constructing this index, we seek a scalar measure built from n critical rate parameters. There will be, then, an $n \times n$ matrix \mathbf{Z} of ‘main’ and ‘interaction’ effects analogous to – but perhaps much different from – a correlation matrix. That is, the matrix \mathbf{Z} is not likely to be symmetric.

It is, however, possible to determine n matrix invariants r_i according to the standard polynomial construction

$$p(\gamma) = \det(\mathbf{Z} - \gamma\mathbf{I}) = \gamma^n + r_1\gamma^{n-1} + \dots + r_{n-1}\gamma + r_n \quad (3)$$

where n is the order of the matrix, \det is the determinant, and \mathbf{I} the $n \times n$ identity matrix. The first invariant is the \mathbf{Z} -matrix trace, and the last is \pm the determinant. Based on the n invariants, it becomes possible to construct an appropriate scalar index $Z = Z(r_1, \dots, r_n)$. One analogy is the magnitude of the largest component in a standard Principal Component Analysis.

Matters can become extortionately complicated. See, for example, computational models of mitochondrial function by Wu et al. (2007), who consider 64 state variables and 210 parameters, and by Bazil et al. (2020), considering 73 and 359, respectively. The scalar parameter Z thus encompasses considerable hidden machinery whose unpacking may be central to developing useful statistical models. In particular, it seems likely necessary to extend the formalisms presented here to analogs of Z that are more complicated algebraic objects than scalars. Following Wallace (2021), we will reconsider something of this in more detail at a later stage of the argument.

Feynman (2000), building on work by Bennett, shows how to construct an ideal machine that converts information into useful work, i.e., free energy. This, it turns out, is a central insight: information can be seen as a form of free energy that we now compound, building an iterated free energy Morse Function (Pettini 2007) characterizing a particular coevolutionary ecosystem. This is done using a Boltzmann probability expression.

The first step is to enumerate the high probability developmental pathways available to the system. Taking $j = 1, 2, \dots$, it is possible to define a probability P_j for a particular path j as

$$P_j = \frac{\exp[-H_j/g(Z)]}{\sum_k \exp[-H_k/g(Z)]} \equiv \frac{\exp[-H_j/g(Z)]}{\mathcal{H}(g(Z))} \quad (4)$$

where $\mathcal{H}(g(Z))$ is this development’s analog to the usual statistical mechanical partition function (Landau and Lifshitz 1980).

The analysis applies to nonergodic as well as to ergodic information sources and can be used for systems in which each developmental pathway x_j has its own source uncertainty measure H_{x_j} . Again, this value can only be defined as a ‘Shannon entropy’ for an ergodic system.

The ‘temperature’ analog $g(Z)$ in the expression has to be calculated from first principles. We will do so by imposing Onsager-like system dynamics built from the partition function.

A classic Morse Function (Pettini 2007) ‘iterated free energy’ F can be written in terms of the partition function denominator of Eq.(4) as

$$\begin{aligned} \exp[-F/g(Z)] &\equiv \sum_k \exp[-H_k/g(Z)] = \mathcal{H}(g(Z)) \\ F &= -\log[\mathcal{H}(g(Z))]g(Z) \\ g(Z) &= \frac{-F}{\text{RootOf}(\exp[Y] - \mathcal{H}(-F/Y))} \end{aligned} \quad (5)$$

If $\mathcal{H}(g(Z)) = g(Z)$ then $g(Z) = -F/W(n, -F)$, where $W(n, x)$ is the Lambert W-function of order n that satisfies the relation $W(n, x) \exp[W(n, x)] = x$. It is real-valued only for $n = 0, -1$ respectively over the ranges $x \geq -\exp[-1]$ and $-\exp[-1] \leq x \leq 0$.

The RootOf construction is thus to be interpreted as a generalized Lambert W-function.

This result is deceptively simple, having a number of deep and subtle implications:

(1). The RootOf construction may have complex number solutions so that the temperature-analog function $g(Z)$ must be taken as analogous to the highly counterintuitive Fisher Zeros that characterize phase transitions in physical systems (Dolan et al. 2001; Fisher 1965; Ruelle 1964).

(2). Since information sources are fundamentally dissipative – palindromes are vanishingly rare and directed homotopy dominates – microreversibility is impossible. As a direct consequence, there can be no ‘Onsager Reciprocal Relations’ in systems of dimension greater than one.

(3). F , as a Morse Function, is subject to symmetry-breaking transitions as $g(Z)$ varies (Pettini 2007). The symmetries here, however, are not those of physical phase transitions most often represented by standard group structures. Information system phase change involves punctuated transitions between equivalence classes of high probability, path-dependent and directed signal sequences, necessarily represented as groupoids. Groupoids are extensions of ‘ordinary’ algebraic groups in which a product is not necessarily defined for every possible pair of elements (Brown 1992; Cayron 2006; Weinstein 1996). The emergence of groupoids appears to be a consequence of the inherently one-way directed homotopy of information sources.

That is, for coevolutionary phenomena, groupoid symmetries are inherent to the directed homotopy-induced by failure of local time reversibility for information systems. This occurs because palindromes have vanishingly small probability. For example, in English, ‘the’ has meaning in context while ‘eht’ has vanishingly low probability in real-world communication.

More complicated information systems may even require more general structures, such as small categories or semigroupoids, further complicating analogs to the standard symmetry-breaking dynamics of physical systems.

Thus there may be a number of phase analogs available to a coevolutionary system as $g(Z)$ varies.

Dynamic behavior of coevolutionary phenomena in our formulation can now be derived via an Onsager approximation in the gradient of an iterated entropy-like measure constructed from the iterated free energy Morse Function F via a Legendre

transform, in a curiously familiar manner (de Groot and Mazur 1984).

We define an ‘entropy’ in terms of the iterated free energy F as

$$S(Z) \equiv -F(Z) + Z dF(Z)/dZ \quad (6)$$

and take the time derivative of Z as defined – in first order – by the gradient in S :

$$\partial Z/\partial t \approx \mu \partial S/\partial Z = Z d^2 F/dZ^2 \quad (7)$$

absorbing the ‘diffusion coefficient’ μ .

Here, it becomes possible to introduce stochastic effects via the Ito Chain Rule (Protter 2005) applied to the basic stochastic differential equation (SDE).

$$dZ_t = (Z_t d^2 F/dZ^2) dt + \sigma V(Z_t) dB_t \quad (8)$$

where the second term imposes what financial engineering calls volatility in Brownian noise dB_t .

The central complication is that there is no single definition of stability for SDE’s. Is the SDE stable in second order (i.e., variance)? In third order? Exponentially? Does it converge in probability? In the presence of Levy jumps? And so on. Each question has its own answer, often via the Ito Chain Rule. The circumstance is well recognized (e.g., Protter 2005; Appleby et al. 2008; Khasminskii 2012).

Imposing ‘stability in order $Q(Z)$ ’, application of the Ito Chain Rule leads to an averaged nonequilibrium steady state relation $\langle dQ_t \rangle = 0$ that can be solved to find F as

$$F(Z) = - \int \int \frac{\sigma^2 V(Z)^2 d^2 Q/dZ^2}{2Z dQ/dZ} dZ dZ + C_1 Z + C_2 \quad (9)$$

Note that setting $\langle dQ_t \rangle = 0$ generates a close analog to the asymptotic stochastic stationary states – the many ‘fixed points’ – of Dieckmann and Law (1996).

Again, these will be structured very exactly by the environmental imposition of ‘stability’ as a selection pressure.

Taking $V(Z) = Z$, a usual expression for volatility in financial engineering SDE’s, leads to the relation for stochastic stability in second order – so that $Q(Z) = Z^2$ – as

$$F(Z) = -\frac{\sigma^2}{4} Z^2 + C_1 Z + C_2 \quad (10)$$

This expression can now be used to characterize $g(Z)$ in Eq.(5), depending in detail on the partition function $\mathcal{H}(g(Z))$.

A direct implication of this result is that the ‘simplicity’ of enforced stability (in second order or otherwise) must be expressed through an enforced complexity in the biological regulatory apparatus necessary to implement it under selection pressure.

An indirect implication is that stability under ‘non-Brownian’ colored noise – realistically, not having a uniform spectral density – will be significantly more complicated (Protter 2005; Hanggi and Jung 1995; Wallace 2016b). Indeed, noise color will likely prove to be an important part of both environmental effects and selection pressures that cannot be represented as information sources Y and S_P in Eq.(2). We do not address this question here, but Wallace (2016b) raises the caution

...[I]f evolutionary process can exapt some phenomenon to evade selection pressure, it usually does, at some point and under some circumstances. Experimental and observational tests may, however, be subtle, if only for ideological reasons because we do not like to think that ‘noise’ itself might carry useful information. We may be missing something of no small biological significance.

Some of this is described in the Mathematical Appendix.

4. Examples

First

Consider a system where the sum in the denominator of Eq.(4) – the partition function – can be approximated as an integral across a limited venue of source uncertainties, so that, for small δ ,

$$\begin{aligned} \exp[-F/g] &= \int_0^\delta \exp[-H/g] dH = \\ &g(1 - \exp[-\delta/g]) \\ L &\equiv \frac{\int_{H_0}^\delta \exp[-H/g] dH}{\int_0^\delta \exp[-H/g] dH} = \\ &\frac{-e^{-\frac{H_0}{g}} + e^{-\frac{\delta}{g}}}{e^{-\frac{\delta}{g}} - 1} \end{aligned} \quad (11)$$

where F is the free energy analog and L represents a ‘rate of reaction’ for a triggering ‘activation energy’ threshold $H_0 < \delta$ (Laidler 1987).

Imposing the further approximation

$$\exp[-\delta/g] \approx 1 - \frac{\delta}{g} + \frac{\delta^2}{2g^2}$$

some algebra finds

$$g(F) = \frac{\delta F}{\delta W\left(n, -\frac{2F e^{-\frac{2F}{\delta}}}{\delta^2}\right) + 2F} \quad (12)$$

where, again, $W(n, x)$ is the Lambert W -function of order n , real-valued only for $n = 0, -1$ over limited ranges in x . For $n = 0$, the real-value range is $-\exp[-1] \leq x$, and for $n = -1$, $-\exp[-1] \leq x \leq 0$. Here, $x = -2F \exp[-2F/\delta]/\delta^2$, constraining the interaction of F and δ .

We wish to determine the dynamics of g under uncertainty, specifically focusing on the nonequilibrium steady state corresponding to second-order stability, using Eq.(10), taking

$$F(Z) = -\frac{Z^2}{4} + 4Z$$

setting $\delta = 0.1$, $\sigma = 1$. Examining the real and imaginary $n = 0$ and $n = -1$ solutions together generates the unexpected bifurcation pattern of figure 1.

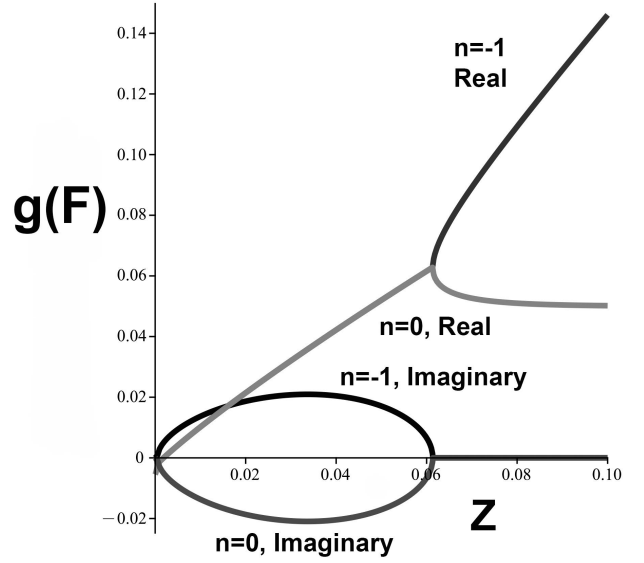


Figure 1: An unexpected bifurcation. These are second-order nonequilibrium steady state stability solutions for $g(F)$ from Eq.(10), setting $F = -(Z^2/4) + 4Z$, with $\delta = 0.1$. Here, $\sigma = 1$, with $n = -1, 0$ in the Lambert W -function. Nonzero imaginary components preclude stability, which emerges for both components at a critical scalar resource rate $Z \approx 0.06136$, where the imaginary components both converge on zero. Above that resource rate, however, there are two stable solutions, one showing relentless increase in evolutionary temperature with resource richness. The second mode, however, converges on a relatively low stable level (0.05), in spite of increasing resource rate. The imaginary-valued ‘loop’ divides Z into two equivalence classes, defining a groupoid whose symmetry-breaking – in terms of ‘Fisher zeros’ – characterizes phase transition.

Nonzero imaginary components preclude stability, which – surprisingly – emerges for both components at a critical scalar resource rate $Z \approx 0.06136$, where the imaginary components both converge on zero. Above that resource rate, however, there are two stable solutions, one showing relentless monotonic increase in evolutionary temperature with resource richness. The second mode, however, rapidly converges on a fixed, stable, but much lower level, in spite of increasing resource rate.

These results are consistent with – and indeed explicitly illustrate – the vagaries of the critical *RootOf* expression in Eq.(5).

However, here, as always, scale counts. Figure 1 is confined to near zero Z for a fixed value of σ at $\delta = 0.1$. Keeping the same value for δ , but taking $F = -\sigma^2 Z^2/4 + 4Z$, allowing σ to vary, and driving Z far beyond the origin, produces figure 2a.

Higher values of Z are expressed in the $n = -1$ component, strongly influenced by variation in σ . That is, the resource rate Z and the ‘noise level’ σ are synergistic in determining system dynamics. The imaginary-valued components remain zero.

It is of interest to take a section through figure 2a at $\sigma = 1$, allowing Z to vary. This is shown in figure 2b. The resulting inverted-U signal transduction form implies that coevolutionary process – in this model approximation – will be subject to eutrophication at very high resource rates. The ‘reaction rate’ L from Eq.(11) will likewise follow an inverted-U pattern.

This is a different world.

It is worth noting that the imaginary-valued ‘loop’ in figure

1 divides Z into two equivalence classes, automatically defining a groupoid whose symmetry-breaking – in terms of the ‘Fisher zeros’ – characterizes phase transitions. Similarly, obvious sets of $\{Z, \sigma\}$ in figure 2 divide the base plane into equivalence classes defining a groupoid whose ‘symmetry-breakings’ also represent analogs to Fisher Zero phase transitions.

Second

The second model examines a system split into only two levels, having source uncertainties $H \pm \delta$, with δ again assumed small. The partition function/free energy relation is just

$$\exp[-F/g] = \exp[-(H + \delta)/g] + \exp[-(H - \delta)/g] \quad (13)$$

Expanding this to second order in δ and solving for g gives two solutions as

$$g^\pm \approx -\frac{F - H \pm \sqrt{-2 \ln(2) \delta^2 + F^2 - 2FH + H^2}}{2 \ln(2)} \quad (14)$$

Setting $F = -Z^2/4 - 4Z + 1$ according to Eq.(10) – taking $\sigma = H = 1$, $\delta = 0.1$ – gives figure 3, closely analogous to figure 1. Again, imaginary components collapse to zero at a critical value of Z , and the real-valued components either increase with Z or fall to a steady-state value. This behavior can also be interpreted as Fisher zero/groupoid symmetry-breaking.

Again, (Laidler 1987) if H in Eq.(13) can be viewed as an generalized ‘activation threshold’ below which no system transition takes place, then a kind of reaction rate can be calculated in a standard manner as

$$L(F) = \frac{\exp[-(H + \delta)/g(F)]}{\exp[-(H + \delta)/g(F)] + \exp[-(H - \delta)/g(F)]} = \frac{1}{1 + \exp[2\delta/g(F)]} \quad (15)$$

Taking the same parameters as in figure 3 gives figure 4. System reaction rate analogs thus endure similar instabilities under stochastic burden and resource rate limitations. Focusing on the life-course trajectories of individual organisms, this suggests models of the onset of pathology under stress or aging (Wallace 2022).

Third

Rather than only two levels as in the example of figure 3, suppose there are two sets of N each, distributed at random above and below a critical observational level H_0 . The partition function F is determined by

$$\exp[-F/g] = \sum_{j=1}^N \exp[-(H_0 + \delta_j)/g] + \sum_{i=1}^N \exp[-(H_0 - \delta_i)/g] \quad (16)$$

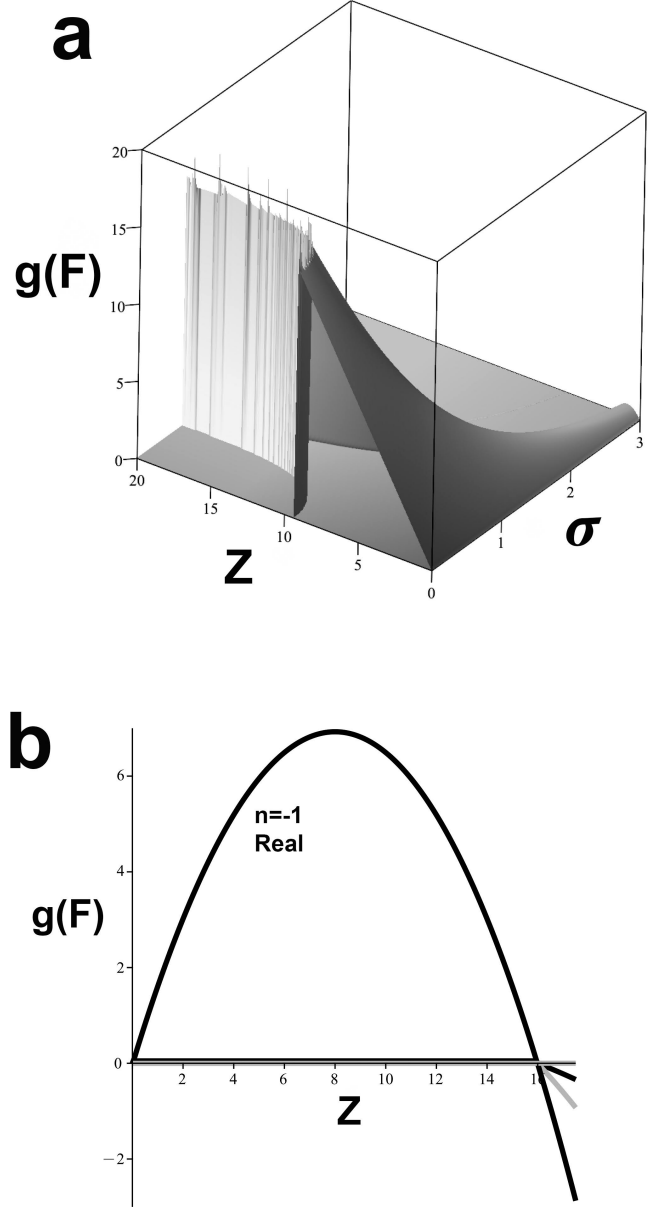


Figure 2: Scale counts. (a) Letting σ vary and forcing Z far beyond the origin presents a different picture, with the real-valued, $n = -1$ component dominating, but strongly sculpted by σ . Such synergism represents a different world. Again, sets of $\{Z, \sigma\}$ in the base plane divide into equivalence classes defining a groupoid whose ‘symmetry-breakings’ are analogous to Fisher Zero phase transitions. (b) A cross section of (a) at $\sigma = 1$. This particular model of coevolution is subject to signal transduction ‘inverted-U’ eutrophication at high resource rates. The ‘reaction rate’ L from Eq.(11) will likewise follow an inverted-U with increasing Z .

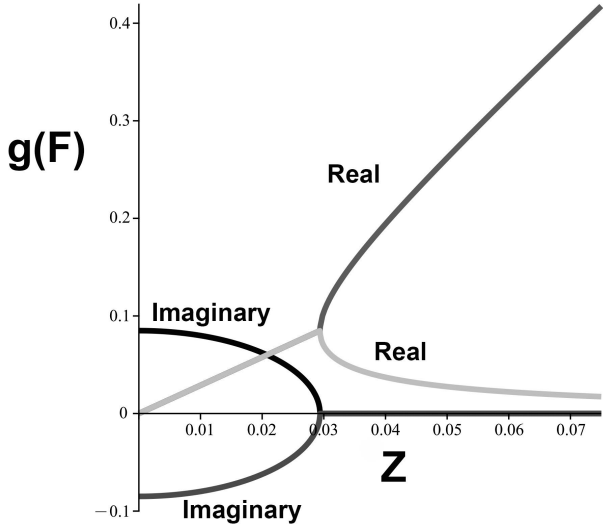


Figure 3: Analog to figure 1, using the relations of Eq.(13) and (14). Here, $F = -Z^2/4 - 4Z + 1$, with $\sigma = H = 1$ and $\delta = 0.1$. Again, a bifurcation indicates a Fisher zero/groupoid symmetry-breaking at a critical value of the resource rate Z .

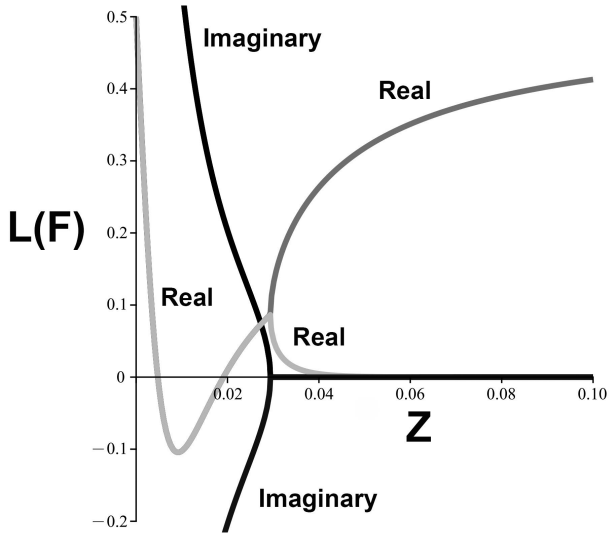


Figure 4: The 'reaction rate' of Eq.(15) corresponding to figure 3. Reaction rates thus endure instability under stochastic burden and resource rate limitations.

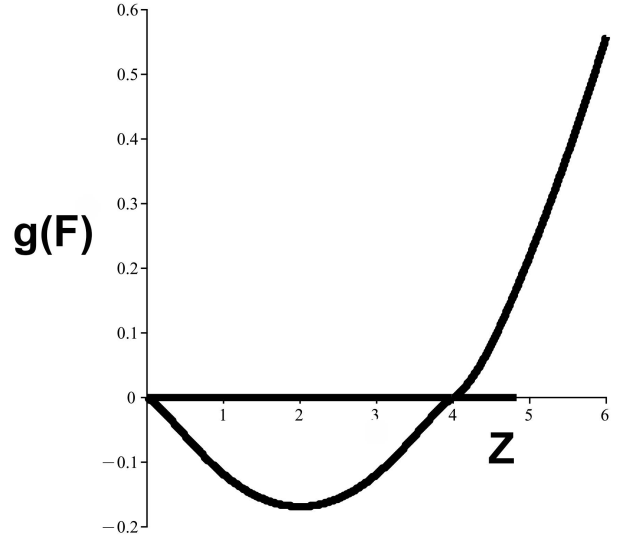


Figure 5: Analog to figures 1 and 3 for the relations of Eqs.(17) and (18). The numerical solution misses imaginary valued points, but phase transitions are evident.

Making the approximation $\exp[\delta/g] \approx 1 + \delta/g + \delta^2/2g^2$ for small δ and collecting terms, under the assumption that the δ themselves sum to zero, gives

$$\exp[-F/g] \approx \exp[-H_0/g] \left(2N + \frac{\Delta}{2g^2} \right) \quad (17)$$

where $\Delta \equiv \sum_{k=1}^{2N} \delta_k^2$. That is, the sum is taken over all δ_k .

This expression can be solved numerically for g , using Eq.(10). Here, we take $\sigma = 1$, now, however, defining

$$F = \frac{-Z^2}{4} + Z + 1 \quad (18)$$

with $H_0 = 1$, $N = 100$, $\Delta = 10$, to give figure 5.

The overall form is different from the previous examples, with the numerical procedure, *implicitplot* in the computer algebra program Maple 2022, missing imaginary components. Nonetheless, phase transitions are still evident.

As $\Delta \rightarrow 0$, the system can be approximated by an expression much like Eq.(14), leading to a version of figure 3, as might be expected.

Fourth

Reconsidering the first example, if $\delta \rightarrow \infty$, then

$$\begin{aligned} \exp[-F/g] &= \int_0^\infty \exp[-H/g] dH = g \\ g &= \frac{-F}{W(n, -F)} \\ L(F) &\equiv \frac{\int_{H_0}^\infty \exp[-H/g] dH}{\int_0^\infty \exp[-H/g] dH} = \exp[-H_0/g(F)] \end{aligned} \quad (19)$$

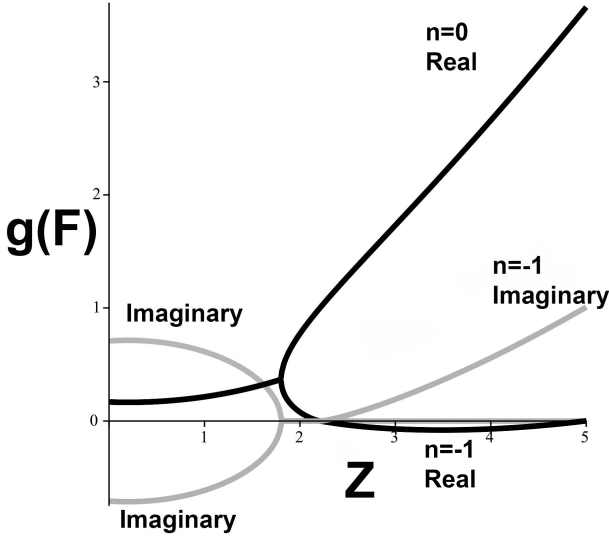


Figure 6: Analog to figures 1 and 3 for the model of Eq.(19). Here, imposing second order stability through Eq.(10), $F = -Z^2/4 + Z/10 + 1$.

where $W(n, F)$ is again the Lambert W-function of order n and $L(F)$ recapitulates the ‘reaction rate’ calculations of Eqs.(11) and (15)

Setting $\sigma = 1$ and taking $F = -Z^2/4 + Z/10 + 1$ generates figure 6, analogous to figures 1 and 3. Again, recall that we have imposed second-order stability through Eqs.(9) and (10).

In figure 7 we continue the development toward something much like figure 2a, but in terms of the cognition rate $L = \exp[-H_0/g(F)]$, imposing second-order stability, and setting $H_0 = 1$, with $F = -\sigma^2 Z^2/4 + Z/10 + 1$ and $n = 0$. The necessary condition for real-value in the Lambert W-function of zero order, $-F \geq -\exp[-1]$, limits possible ranges of σ and Z .

5. Extending the models

We have assumed systems as fully characterized by the single scalar parameter Z , mixing material resource/energy supply with internal and external flows of information. Following Wallace (2021) – invoking techniques akin to Principal Component Analysis – it can be argued that there may often be more than one independent composite entity irreducibly driving system dynamics. Consequently, it may often be necessary to replace the scalar Z with an n -dimensional vector \mathbf{Z} having orthogonal components that, together, account for most of the total variance in the rate of supply of essential resources. The basic dynamic equations then become considerably more complicated,

$$\begin{aligned} F(\mathbf{Z}) &= -\log(\mathcal{H}(g(\mathbf{Z})))g(\mathbf{Z}) \\ S &= -F + \mathbf{Z} \cdot \nabla_{\mathbf{Z}} F \\ \partial \mathbf{Z} / \partial t &\approx \hat{\mu} \cdot \nabla_{\mathbf{Z}} S = f(\mathbf{Z}) \\ -\nabla_{\mathbf{Z}} F + \nabla_{\mathbf{Z}} (\mathbf{Z} \cdot \nabla_{\mathbf{Z}} F) &= \\ \hat{\mu}^{-1} \cdot f(\mathbf{Z}) &\equiv f^*(\mathbf{Z}) \end{aligned}$$

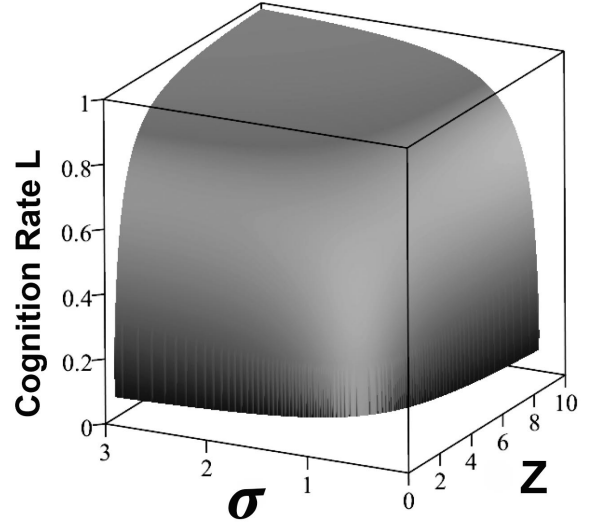


Figure 7: Analog to figure 2a for the cognition rate L in Eq.(19), under second-order stability. Here, $H_0 = 1$, $F = -\sigma^2 Z^2/4 + Z/10 + 1$, $n = 0$. The necessary condition for real-value in the Lambert W-function of zero order is $-F = \sigma^2 Z^2/4 - Z/10 - 1 \geq -\exp[-1]$.

$$\begin{aligned} \left(\left(\frac{\partial^2 F}{\partial z_i \partial z_j} \right) \right) \cdot \mathbf{Z} &= f^*(\mathbf{Z}) \\ \left(\left(\frac{\partial^2 F}{\partial z_i \partial z_j} \right) \right) |_{\mathbf{Z}_{nss}} \cdot \mathbf{Z}_{nss} &= \mathbf{0} \end{aligned} \quad (20)$$

F , g , \mathcal{H} , and S are scalar functions, while $\hat{\mu}$ is an n -dimensional square matrix of diffusion coefficient analogs.

The expression $\left(\left(\frac{\partial^2 F}{\partial z_i \partial z_j} \right) \right)$ is an n -dimensional square matrix of second partial derivatives, and $f(\mathbf{Z})$ is a vector function. The last relation imposes a deterministic nonequilibrium steady state condition, i.e. $f^*(\mathbf{Z}_{nss}) = \mathbf{0}$. This may or may not be inherently stable.

Taking a particularly simple approach, $\mathcal{H}(g(\mathbf{Z})) \rightarrow g(\mathbf{Z})$, with $\mathbf{Z}(t) \rightarrow \mathbf{Z}_{nss}$.

This is an overdetermined system of partial differential equations (Spencer 1969) if $n \geq 2$. Indeed, for a general $f^*(\mathbf{Z})$, the system is inconsistent, resulting in as many as n different expressions for $F(\mathbf{Z})$, and hence the same number of temperature-analog measures.

This inference should not be surprising. The fifth expression in Eq.(20), where $f^*(\mathbf{Z}) \neq \mathbf{0}$, represents, most generally, a multi-component, cross-interacting, cross-talking, system that, if acting in real time, will almost always be far indeed from any steady state, equilibrium or nonequilibrium.

Such systems will almost always be inherently unstable, requiring constant input of control information that will necessarily lag perturbation. Such a structure should not, in fact, be characterizable by a single cognitive temperature-analog g . Each cognitive component, if the system is far from a steady state, should be expected to have its own g -value, in addition to structure imposed by the multidimensional nature of \mathbf{Z} .

The vector function $f(\mathbf{Z})$ becomes the basis for extension of Eq.(8) as a multi-dimensional SDE having the form

$$d\mathbf{Z}_t = f(\mathbf{Z}_t)dt + \rho(\mathbf{Z}_t)d\mathbf{B}_t \quad (21)$$

where $d\mathbf{B}_t$ represents n -dimensional Brownian noise.

This development, where the dimension is $n \geq 2$, invokes the world of Appleby et al. (2008), in which it is almost always possible to find a functional form $\rho(\mathbf{Z})$ that destabilizes an inherently stable function $f(\mathbf{Z})$, or – by contrast – stabilizes an inherently unstable one.

In addition, as Wallace (2021) shows, higher dimensional systems suffer the burdens of Lie Group methods in the study of their deterministic dynamics.

Likewise, as discussed above, Eqs.(9) and (21) can be extended to systems with colored noise, via the Dolean-Dade exponential, contingent on no small algebraic overhead (Protter 2005; Wallace 2016b).

6. Selection pressure as shadow price

Central to gene frequency evolutionary models and their EES extensions is the idea of optimization on a ‘fitness landscape’ or on paths constrained within such a landscape (e.g., Gonzalez-Forero and Gardner 2021, 2022). More generally, we can seek to maximize some index of critical function across a multi-component system constrained by resource rates and by the necessity of responding collectively to environmental signals or changes within time constraints. An essential feature is an assumption that the rate at which an essential resource is delivered to component i is governed according to Eq.(7) as

$$\partial Z_i / \partial t = dS / dZ_i = f_i(Z_i) \quad (22)$$

The full system is seen as consisting of $i = 1, 2, \dots, m$ cooperating units that must be individually supplied with resources at rates Z_i under the overall constraints of resources and time as $\sum_i Z_i = Z$, $\sum_i T_i = T$. We then optimize some critical scalar index of function across the full system under these constraints.

As an example, we take the sum of subcomponent cognition rates of Eqs.(11), (15), and (19), assuming $dZ_i/dt = f(Z_i) \rightarrow 0$.

While more general approaches to optimization than simple Lagrangian are possible (e.g., Nocedal and Wright 2006), here we construct a general Lagrangian optimization across subcomponent cognition rates as

$$\begin{aligned} \mathcal{L} &= \sum_i L_i + \lambda \left(Z - \sum_i Z_i \right) + \mu \left(T - \sum_i T_i \right) \\ \partial \mathcal{L} / \partial Z &= \lambda \\ \partial L_i / \partial Z_i &= \lambda \\ \partial L_i / \partial T_i &= \mu \end{aligned} \quad (23)$$

remembering in particular that $\partial Z_i / \partial T_i = f_i(Z_i)$.

In simple economic models, λ and μ represent the ‘shadow prices’ imposed on system dynamics by environmental constraints, in a large sense (Jin et al. 2008; Robinson 1993).

While many such formalisms are possible, simple Lagrangian optimization serves to outline the underlying canonical mechanism.

Algebraic manipulation – which will apply to virtually all possible scalar function measures – gives

$$\begin{aligned} f_i(Z_i) &= \frac{\mu}{\lambda} \\ Z_i &= f_i^{-1}\left(\frac{\mu}{\lambda}\right) \end{aligned} \quad (24)$$

so that a monotonic function $f_i(Z_i)$ generates a monotonic dependence of Z_i on the shadow price ratio.

For example, setting $f_i(Z_i) = \beta_i - \alpha_i Z_i$ – an ‘exponential’ model – produces the expression

$$Z_i = \frac{\beta_i - \mu/\lambda}{\alpha_i} \quad (25)$$

Sufficient environmental shadow price burden – selection pressure – will drive any component resource rate Z_i below what is needed for critical modular function.

Shadow prices characterize environmental burdens – selection pressures – leading to decline in the maximum possible level of resource delivery Z_{max} below some critical value Z_{crit} . Optimization becomes impossible, and we could then write both Z_{max} and Z_{crit} for a critical subsystem as appropriate functions of some integral of the environmental shadow price over the duration of acute selection pressure. Details will vary across organisms and environments, with optimization model and measures of λ , μ and Z , but the mechanism seems canonical.

Rather than cognition rates, another approach would be to take the free energy analog $F(\mathbf{Z})$ from Eq.(20) as the direct basic scalar index, seeking Lagrangian stationary points – minimization, perhaps – based on the relation

$$((\partial^2 F / \partial Z_i \partial Z_j)) \cdot \mathbf{Z} = \hat{\mu}^{-1} \cdot f(\mathbf{Z})$$

from Eq.(20). While much depends on the properties of the Hessian matrix of the full optimization – dependent, in turn, on this expression – shadow prices still impose selection pressure, as they would for any possible scalar measure of function in this formulation.

7. Discussion

We have outlined a modestly comprehensive, ‘mathematically elegant’ formulation of the Extended Evolutionary Synthesis. Here, while gene frequencies are not predominant, they do not go away. Rather, as the ‘message’ in the transmission of genetic information, they become words emitted by a particular heritage information source interacting with others representing embedding ecosystems, niches, cognition, in a large sense, with its associated regulatory agencies, other heritage mechanisms, characteristic large deviations, and structured selection pressures.

All of this occurs within the context of a surprisingly influential stochastic burden in which requirement for stability at a particular order – codified in Eq.(9) – actually sets nonequilibrium steady states, as based on Onsager models in which time derivatives of essential parameters are determined by parameter gradients in an entropy analog built from a free energy index.

One implication of this result is that the draconian simplicity of enforced stochastic stability is inevitably and inversely implemented by an explosion of the complex bioregulatory machineries necessary to impose it.

We reiterate that, in this formulation, there can be additional heritage information sources beyond genetic. These may be biochemical epigenetic or, in higher animals, cultural (e.g., Jablonka and Lamb 1998; Jaenisch and Bird 2003; Avital and Jablonka 2000; Heine 2001).

Comprehensive formulations in terms of the asymptotic limit theorems of probability theory permit construction of both mathematical models and statistical tools providing benchmarks against which to compare observational and experimental data (Pielou 1977, 1981). Such comparison encourages interplay between theory and data, contingent on a rigid determination not to fossilize scientific enterprise within the amber of any particular mathematical structure, however elegant.

Indeed, some do not find that gene frequency models embody much notable mathematical elegance: *de gustibus non disputandum est*.

The reader may not agree with the particular approach taken here, but this work does suggest that the EES can indeed be mathematically formalized in a comprehensive and ‘elegant’ manner. Working out useful regression model analogs from any such theory – and validating their realms of utility – remains typically challenging.

More to the point, as Pielou (1977, 1981) notes, the utility of mathematical models in the study of complex biological and ecological phenomena arises from a dynamic interplay between model-based suggestions and data-based conclusions, a relation in which models and statistical tools, however elegant, must always play a subordinate role.

8. Mathematical Appendix: colored noise

Only a taste. Following Protter (2005), the quadratic variation $[X, Y]_t$ between two continuous stochastic processes can be written in terms of Ito stochastic integrals as

$$X_t Y_t = X_0 Y_0 + \int_0^t X_{s-} dY_s + \int_0^t Y_{s-} dX_s + [X, Y]_t \quad (26)$$

where $s-$ indicates left-continuity. For a discrete process the integrals are rewritten as sums to produce a ‘simpler’ expression.

For Brownian white noise dB_t , $[B_t, B_t] \propto t$. Colored noise will produce a different time dependence.

If an SDE can be written as $dX_t = X_{t-} dY_t$, where Y_t is a stochastic process, the solution is given by the Doleans-Dade exponential as

$$X_t \propto \exp\left(Y_t - \frac{1}{2}[Y, Y]_t\right) \quad (27)$$

By the mean value theorem, if

$$\frac{1}{2}d[Y, Y]/dt > dY/dt \quad (28)$$

then $X_t \rightarrow 0$, remembering that, for Brownian processes, $[Y, Y] \propto t$.

The argument can be directly, if not easily, extended to Levy jump-processes (Protter 2005).

CRedit authorship contribution statement

RW: mathematics, writing. DW: biology and ecology, review.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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