Equations

In the Equations table, the LaTeX plaintext is provided and also it is automatically rendered and copied at the interactive Coda site.

Equations

Section	LaTeX - Math	Description	Equation #	LaTeX	Ontology terms	Notes
A variational formulation 4	$\tilde{\pi}$	path of a phenotype			phenotype, path	
	$\bar{\pi}$	relevant variables at the evolutionary scale			Evolution, EcoEvoDevo	
	$\bar{\pi}_n^{(i)} = \mathbf{R} \circ \tilde{\pi}_n^{(i)}$	bottom-up causation is simply the application of a reduction operator to select variables that change very slowly			causality	
	$\{\pi_n^{(i+1)}\} = \mathbf{G} \circ \{\bar{\pi}_n^{(i)}\}$	Top-down causation entails a specification of fast phenotypic trajectories in terms of slow genotypic variations, which are grouped into populations, , according to the influences they exert on each other			causality	
Particular partitions 17	$\dot{x} = f_{\bar{x}}(x) + \omega = \begin{bmatrix} \dot{\eta} \\ \dot{s} \\ \dot{a} \\ \dot{\mu} \end{bmatrix} = \begin{bmatrix} f_{\bar{\eta}}(\eta, s, a) \\ f_{\bar{s}}(\eta, s, a) \\ f_{\bar{a}}(s, a, \mu) \\ f_{\bar{\mu}}(s, a, \mu) \end{bmatrix} + \begin{bmatrix} \omega_\eta \\ \omega_s \\ \omega_a \\ \omega_\mu \end{bmatrix}$	The evolution of these sparsely coupled states can be expressed as a Langevin or stochastic differential equation; namely, a high dimensional, nonlinear, state-dependent flow plus independent random (Wiener) fluctuations, , with a variance of 2Γ	1		Evolution, states, flow, Stochastic	
	$\begin{bmatrix} f_{\bar{\eta}}(\eta, b) \\ f_{\bar{s}}(\eta, b) \\ f_{\bar{a}}(b, \mu) \\ f_{\bar{\mu}}(b, \mu) \end{bmatrix} = \begin{bmatrix} Q_\eta - \Gamma_\eta & Q_{\eta s} & . & . \\ -Q_{\eta s}^T & Q_s - \Gamma_s & . & . \\ . & . & Q_a - \Gamma_a & Q_{a\mu} \\ . & . & -Q_{a\mu}^T & Q_\mu - \Gamma_\mu \end{bmatrix} \begin{bmatrix} \nabla_\eta \Im(\eta \mid b) \\ \nabla_s \Im(\eta \mid b) \\ \nabla_a \Im(b \mid \mu) \\ \nabla_\mu \Im(b \mid \mu) \end{bmatrix}$	The flow of Equation 1 can be expressed using the Helmholtz decomposition (expressing the flow as a mixture of a dissipative, gradient flow and a conservative, solenoidal flow)	2		flow, solenoidal	
	$[x(t)] \subset \tilde{x}$	the history or path of a time varying state			path, time, State	
	$f_{\bar{x}}(x)$	the paths of a state-dependent flow are determined by state-dependent flow			State	

$\bar{x} \subset \tilde{x}$	Parameters of the state-dependent flow	State, parameter, flow
$x(0) = x_0 \subset \bar{x}$	Initial states of parameters of the state-dependent flow	parameter, State, flow
$x = (\eta, s, a, \mu)$	Partition of states comprising the external, sensory, active and internal states of a phenotype	External State, Active States, Internal State, Sense State, phenotype, Partition
$b = (s, a)$	Sensory and active states constitute *blanket* states	Sense State, Active States, Blanket State
$\pi = (b, \mu) = (s, \alpha)$	*phenotypic* states comprise internal and blanket states	phenotype, Internal State, Blanket State
$\alpha = (a, \mu)$	The *autonomous* states of a phenotype are not influenced by external states:	State, phenotype, External State
ω	independent random (Wiener) fluctuations	random
Γ	Variance of independent random (Wiener) fluctuations is 2Γ.	Variance, random
$\Gamma \nabla \Im$	gradient flow (depends upon the amplitude of random fluctuations)	
$Q \nabla \Im$	solenoidal flow (circulates on the isocontours of potential function called *self-information*)	
$\Im(x) = -\ln(p(x))$	self-information	

		$p(x)$	the nonequilibrium steady-state density (NESS density)	
		$\dot{s}^{(i+1)} = f_{\bar{s}}(\eta, s, a) + \omega$ $\dot{\eta}^{(i+1)} = f_{\bar{\eta}}(\eta, s, a) + \omega$ $\dot{\mu}^{(i+1)} = f_{\bar{\mu}}(s, a, \mu) + \omega$ $\dot{a}^{(i+1)} = f_{\bar{a}}(s, a, \mu) + \omega$ $\{\pi_m^{(i+1)}\} = \mathbf{G} \circ \{\mathbf{R} \circ \tilde{\pi}_n^{(i)}\}$ $\bar{\pi}_\ell^{(i)} \in \bar{\pi}_m^{(i+1)}$ $\dot{s}^{(i)} = f_{\bar{s}}(\eta, s, a) + \omega$ $\dot{\eta}^{(i)} = f_{\bar{\eta}}(\eta, s, a) + \omega$ $\dot{\mu}^{(i)} = f_{\bar{\mu}}(s, a, \mu) + \omega$ $\dot{a}^{(i)} = f_{\bar{a}}(s, a, \mu) + \omega$	**Figure 1**: schematic (i.e., influence diagram) illustrating the sparse coupling among states that constitute a particular partition at two scales	
Ensemble dynamics and paths of least action	10	$\mathfrak{I}(x) = -\ln(p(x))$	self-information or surprisal of a state; namely, the implausibility of a state being occupied. When the state is an allele frequency and evolves according to Wright–Fisher dynamics, this is sometimes referred to as an 'adaptive landscape'	3
		$L(\vec{x}) = -\ln(p(x)) = \frac{1}{2}\left[\ln(\|\Gamma\|) + (\mathbf{D}\vec{x} - f(\vec{x})).\frac{1}{2\Gamma}(\mathbf{D}\vec{x} - f(\vec{x})) + \nabla.f\right]$	the Lagrangian, which is the surprisal of a generalised state; namely, the instantaneous path associated with the motion from an initial state. In generalised coordinates of motion, the state, velocity, acceleration, etc are treated as separate (generalised) states that are coupled through the flow	3
		$\mathbf{A}(\tilde{x}) = -\ln(p(\tilde{x}\|x_0)) = \int \mathbf{L}(\vec{x})dt$	the surprisal of a path is called *action*, namely, the path integral of the Lagrangian.	3
		$\nabla_{\vec{x}}\mathbf{L}(\vec{x}) + \lambda(\vec{x} - \mathbf{D}\vec{x}) = 0 \Longleftrightarrow \vec{x}(\tau) = \mathbf{D}\vec{x} - \frac{1}{\lambda}\nabla_{\vec{x}}\mathbf{L}(\vec{x})$	Generalised states afford a convenient way of expressing the path of least action in terms of the Lagrangian	4
		$\vec{x} = \mathbf{D}\vec{x} = f(\vec{x})$ $\Longleftrightarrow \nabla_{\vec{x}}\mathbf{L}(\vec{x}) = 0 \Longleftrightarrow \vec{x} = \arg\min_{\vec{x}} \mathbf{L}(\vec{x})$ $\Longleftrightarrow \delta_{\tilde{x}}\mathbf{A}(\tilde{x}) = 0 \Longleftrightarrow \tilde{x} = \arg\min_{\tilde{x}} \mathbf{A}(\tilde{x})$	Denoting paths of least action with boldface, this is sometimes described as convergence to the path of least action, in a frame of reference that moves with the state of generalized motion	5
		$\frac{\partial^2 f}{\partial\eta\partial\mu} = 0 \Longleftrightarrow \frac{\partial^2 L}{\partial\vec{\eta}\partial\vec{\mu}} = 0 \Longleftrightarrow L(\vec{\eta}, \vec{\mu}, \|\vec{s}, \vec{a}) = L(\vec{\eta}\|\vec{s}, \vec{a}) + L(\vec{\mu}\|\vec{s}, \vec{a}) \Longleftrightarrow (\vec{\eta} \perp \vec{\mu})\|\vec{s}, \vec{a}$	We can also express the conditional independencies implied by a particular partition using the Lagrangian of generalized states. Because there are no flows that depend on both internal and external states, external and internal paths are independent, when conditioned on blanket paths:	6
		$x(t)$	states	

		$\vec{x} = (x, x', \dots)$	generalised states	
		$\tilde{x} = [x(t)]$	paths	
		λ	λ is the Lagrange multiplier, which ensures the generalized motion of states corresponds to the state of generalized motion. When λ is suitably small, solutions of the implicit generalized equations of motion converge (almost) instantaneously to the path of least action.	
Different kinds of things	9	$\left\{\pi_1^{(i)}, \dots, \pi_N^{(i)}\right\} = \mathbf{G} \circ \left\{ x_1^{(i)}, \underbrace{\underbrace{x_j^{(i)}, \dots, x_k^{(i)}}_{S_n^{(i)}}, \underbrace{x_\ell^{(i)}, \dots, x_m^{(i)}}_{a_n^{(i)}}, \underbrace{x_o^{(i)}, \dots, x_p^{(i)}}_{\mu_n^{(i)}}}_{\pi_n^{(i)}} \right\}$	Group of phenotypes, reflecting particular states in the ensemble of particles in population	7
		$\dot{\pi}_n = \begin{bmatrix} \dot{s}_n \\ \dot{\alpha}_n \end{bmatrix} = \begin{bmatrix} f_{\bar{s}_n}(b_n, \dots, b_N) \\ f_{\bar{\alpha}_n}(b_n, \mu_n) \end{bmatrix} + \omega$	Expression of the dynamics of each particle in terms of its sensory states—that depend upon the blanket states of other particles—and autonomous states—that only depend upon the states of the particle in question	8
		$\begin{bmatrix} f_{\bar{s}_n} \\ f_{\bar{\alpha}_n} \end{bmatrix} = \begin{bmatrix} Q_{s_n} - \Gamma_{s_n} & \cdot \\ \cdot & Q_{\alpha_n} - \Gamma_{\alpha_n} \end{bmatrix} \begin{bmatrix} \nabla_{s_n} \Im(b_1, \dots, b_N) \\ \nabla_{\alpha_n} \Im(\alpha_n \mid s_n) \end{bmatrix}$	Expression of the dynamics of each particle in terms of its sensory states—that depend upon the blanket states of other particles—and autonomous states—that only depend upon the states of the particle in question	8
		$\xrightarrow{\mathbf{R}} \left\{\tilde{x}_\ell^{(i)}\right\} \xrightarrow{\mathbf{G}} \left\{\tilde{\pi}_n^{(i)}\right\} \xrightarrow{\mathbf{R}} \left\{\tilde{x}_n^{(i+1)}\right\} \xrightarrow{\mathbf{G}} \left\{\tilde{\pi}_m^{(i+1)}\right\} \xrightarrow{\mathbf{R}}$	the states in the particular ensemble have to be the states of some ‘thing’; namely, the states of a particle at a lower scale. This means that states must be the states of particles (e.g., phenotypic states) that constitute the particular states at the next scale (e.g., phylogenetic states) This recursive truism can be expressed in terms of grouping G operator—that creates particles—and a reduction R operator—that picks out certain particular states for the next scale	9
		$\xrightarrow{\mathbf{R}\circ\mathbf{G}} \left\{\tilde{\chi}_\ell^{(i)}\right\} \xrightarrow{\mathbf{R}\circ\mathbf{G}} \left\{\tilde{\chi}_n^{(i+1)}\right\} \xrightarrow{\mathbf{R}\circ\mathbf{G}}$ $\xrightarrow{\mathbf{G}\circ\mathbf{R}} \left\{\tilde{\pi}_n^{(i)}\right\} \xrightarrow{\mathbf{G}\circ\mathbf{R}} \left\{\tilde{\pi}_m^{(i+1)}\right\} \xrightarrow{\mathbf{G}\circ\mathbf{R}}$ $\left\{\pi(\tau)_1^{(i+1)}, \dots, \pi(\tau)_M^{(i+1)}\right\} = \mathbf{G} \circ \{\mathbf{R} \circ \tilde{\pi}_1^{(i)}, \dots, \underbrace{\underbrace{\mathbf{R} \circ \tilde{\pi}_j^{(i)}, \dots, \mathbf{R} \circ \tilde{\pi}_k^{(i)}}_{S_m^{(i+1)}}, \underbrace{\mathbf{R} \circ \tilde{\pi}_\ell^{(i)}, \dots, \mathbf{R} \circ \tilde{\pi}_m^{(i)}}_{\alpha_m^{(i+1)}}}_{\pi_m^{(i+1)}}, \dots\}$ $\bar{\pi}_n^{(i)} = \mathbf{R} \circ \tilde{\pi}_n^{(i)}$ $\left\{\pi_m^{(i+1)}\right\} = \mathbf{G} \circ \left\{\bar{\pi}_n^{(i)}\right\}$	The composition of the reduction and grouping operators can be construed as mapping from the states of particles at one scale to the next or, equivalently, from particular states at one scale to the next. In short, creating particles of particles, namely, populations.	10
		$\mathbf{G}$	grouping operator G that partitions the states at the i-th scale of analysis into N particles on the basis of the sparse coupling implied by a particular partition.	

$$\mathbf{R}$$

a reduction R operator—that picks out certain particular states for the next scale.

$$\alpha_{m_n}^{(i+1)} = \mathbf{R} \circ \tilde{\pi}_\ell^{(i)}$$
$$S_{m_k}^{(i+1)}$$
$$\alpha_{m_\ell}^{(i+1)}$$
$$\underbrace{S_\ell^{(i)}, \alpha_\ell^{(i)}}$$
$$\underbrace{\underbrace{\mathbf{R} \circ \tilde{\pi}_j^{(i)}, \ldots, \mathbf{R} \circ \tilde{\pi}_k^{(i)}}_{S_m^{(i+1)}}, \underbrace{\mathbf{R} \circ \tilde{\pi}_\ell^{(i)}, \ldots, \mathbf{R} \circ \tilde{\pi}_n^{(i)}}_{\alpha_m^{(i+1)}}}_{\pi_m^{(i+1)}}$$

Figure 2: schematic showing the hierarchical relationship between particles at scales *i* and *i*+1. For clarity, only sensory and autonomous states are illustrated in blue and pink, respectively. Note that each variable is a (very large) vector state that itself is partitioned into multiple vector states. At scale *i*+1, each particle represents an ensemble, the elements of which are partitioned into autonomous and sensory subsets. At scale *i*, each particle represents an element of an ensemble, which is itself partitioned into sensory and autonomous subsets. The slow states of each element (e.g., phenotype) are recovered by the reduction operator **R**, to furnish the states at the ensemble level (e.g., genotype). A key feature of this construction is that it applies recursively over scales.

$$x^{(i+1)} = (\eta, s, a, \mu)$$

At the phylogenetic scale — a population corresponds to a set of particular kinds (i.e., sensory and autonomous kinds)

Natural selection: a variational formulation 11

$$\begin{aligned}\Im_n^{(i+1)} &= \Im\left(\alpha_n^{(i+1)} | \pi^{(i+1)} \backslash \alpha_n^{(i+1)}\right) \\ &= \mathbf{A}\left(\tilde{\pi}_\ell^{(i)} | \bar{x}_\ell^{(i)} \subset \pi^{(i+1)}\right) = \mathbf{A}_1^{(i)}\end{aligned}$$

if, at non-equilibrium evolutionary steady-state, the likelihood of an agent's genotype is proportional to the likelihood of its phenotypic trajectory (where \ denotes exclusion), then the following holds (Equation 12). 11

$$\vec{\alpha}(\tau)_\ell^{(i)} = \mathbf{D}\vec{\alpha}_1^{(i)} - \nabla_{\vec{\alpha}_\ell^{(i)}} \mathbf{L}_\ell^{(i)} \underbrace{\overbrace{\rightleftharpoons}^{\mathbf{A}_\ell^{(i)} = \int dt \mathbf{L}_\ell^{(i)}}}_{\bar{x}_\ell^{(i)} \subset \pi_m^{(i+1)}} \dot{\alpha}(\tau)_n^{(i+1)} = \left(Q_\alpha^{(i+1)} - \Gamma_\alpha^{(i+1)}\right) \nabla_{\alpha_n^{(i+1)}} \mathbf{A}_\ell^{(i)} + \omega_n^{(i+1)}$$
$$\mathbf{L}(\tau)_\ell^{(i)} = \mathbf{L}\left(\vec{\pi}_\ell^{(i)} | \bar{x}_\ell^{(i)}\right) \qquad \mathbf{A}_\ell^{(i)} = \int_{\tau-T}^{\tau} dt \mathbf{L}(\tau)_\ell^{(i)}$$

An agent's autonomous dynamics can be cast as a gradient descent on a Lagrangian, whose path integral (i.e., action) corresponds to negative fitness. This Lagrangian depends upon the flow parameters (and initial states) supplied by the genotype. The agent's genotype can then be cast as a stochastic gradient descent on negative fitness (i.e., genetic drift) 12

$$\begin{matrix}\dot{\alpha}_\ell^{(i)} = \left(Q_\alpha^{(i)} - \Gamma_\alpha^{(i)}\right) \nabla_{\alpha_n^{(i)}} \Im_\ell^{(i)} + \omega_\ell^{(i)} & & \dot{\alpha}^{(i+1)} = \left(Q_\alpha^{(i+1)} - \Gamma_\alpha^{(i+1)}\right) \nabla_{\alpha^{(i+1)}} \Im^{(i+1)} + \omega^{(i+1)} \\ & \rightleftharpoons & \\ \Im_\ell^{(i)} = \Im\left(\pi_\ell^{(i)} | \bar{\chi}_\ell^{(i)} \subset \pi^{(i+1)}\right) & & \Im_\ell^{(i)} = \Im\left(\pi^{(i+1)}\right)\end{matrix}$$

The existence of a nonequilibrium evolutionary steady-state solution to the density dynamics (at both scales) allows us to express the fast and slow dynamics of agents and their autonomous states in terms of Helmholtz decompositions. 13

$$\nabla_{\alpha_n^{(i+1)}} \Im^{(i+1)} = \nabla_{\alpha_n^{(i+1)}} \Im_n^{(i+1)} = \nabla_{\alpha_n^{(i+1)}} \mathbf{A}_\ell^{(i)}$$

The gradients of surprisal at the slow scale, with respect to any given agent's 'kind' or genotype, are the gradients of action 14

$$\dot{\vec{\alpha}}_\ell^{(i)} = \mathbf{D}\vec{\alpha}_\ell^{(i)} - \nabla_{\vec{\alpha}_\ell^{(i)}} \mathbf{L}\left(\vec{\pi}_\ell^{(i)} | \bar{x}_\ell^{(i)}\right)$$

In the limit of small fluctuations, the autonomous paths become the paths of least action; i.e., when the fluctuations take their most likely value of zero. 15

$$(i+1)$$

the genotypic state of the n-th agent

		α_n		
		$\pi_{\ell}^{(i)}$	the phenotypic state of the n-th agent	
		$p\left(\overrightarrow{\eta} \middle\| \bar{x}\right)$	the action (i.e., negative fitness) scoring the accumulated evidence. This evidence is also known as a *marginal likelihood* because it marginalises over external dynamics; i.e., other agents.	
		$p\left(\overrightarrow{\eta}, \overrightarrow{\pi} \middle\| \bar{x}\right)$	a phenotype's generative model	
		$\bar{x}$	the extended genotype	
		$\eta(0)_{\ell}^{(i)} \subset \bar{\eta}_{\ell}^{(i)}$	the extended genotype covers both the genetic and epigenetic specification of developmental trajectories and the initial conditions necessary to realise those trajectories, including external states conditions necessary for embryogenesis.	
The sentient phenotype	5	$\dot{\vec{\alpha}} = \mathbf{D}\vec{\alpha} - \nabla_{\vec{\alpha}} F\left(\vec{\alpha}, \vec{s}\right)$ $F\left(\vec{\alpha}, \vec{s}\right) = \underbrace{\mathbb{E}_{p_{\vec{\mu}}}\left[\mathcal{L}_{\vec{\chi}}\left(\vec{\eta}, \vec{s}, \vec{\alpha}\right)\right]}_{\text{Energy constraint}} - \underbrace{\mathbb{E}_{p_{\vec{\mu}}}\left[\mathcal{L}_{\vec{\chi}}\left(\vec{\eta}\right)\right]}_{\text{Entropy}}$ $= \underbrace{D_{KL}\left[p_{\vec{\mu}}\left(\vec{\eta}\right) \| p_{\vec{\chi}}\left(\vec{\eta} \| \chi_0\right)\right]}_{\text{Complexity}} + \underbrace{\mathbb{E}_{p_{\vec{\mu}}}\left[\mathcal{L}_{\vec{\chi}}\left(\vec{s}, \vec{\alpha} \| \vec{\eta}\right)\right]}_{\text{---Accuracy}}$ $= \underbrace{D_{KL}\left[p_{\vec{\mu}}\left(\vec{\eta}\right) \\| p_{\vec{\chi}}\left(\vec{\eta} \| \vec{s}, \vec{a}, \chi_0\right)\right]}_{\text{Divergence}} + \underbrace{\mathcal{L}_{\bar{\chi}}\left(\vec{s}, \vec{\alpha}\right)}_{\text{---Log evidence}}$ $\mathcal{L}_{\bar{\chi}}\left(\vec{\chi}\right) \triangleq -\ln p_{\vec{\chi}}\left(\vec{\chi} \| \chi_0\right)$	variational free energy functional of Bayesian beliefs—about external states—encoded by their internal phenotypic states, under a generative model encoded by their genotype.	16
		$p_{\vec{\mu}}\left(\vec{\eta}\right) \triangleq p_{\bar{x}}\left(\vec{\eta} \| \vec{s}, \vec{\mathbf{a}}, x_0\right) = p_{\bar{x}}\left(\vec{\eta} \| \vec{s}, \vec{\mathbf{a}}, \vec{\mu}, x_0\right)$ $\vec{\alpha} = \arg\min_{\vec{\alpha}} L_{\bar{x}}\left(\vec{\alpha} \| \vec{s}\right) \implies$ $\vec{\mu} = \arg\min_{\vec{\mu}} L_{\bar{x}}\left(\vec{\mu} \| \vec{s}, \vec{\mathbf{a}}\right)$ $\vec{\mathbf{a}} = \arg\min_{\vec{a}} L_{\bar{x}}\left(\vec{a} \| \vec{s}, \vec{\mu}\right)$	We can consider the conditional density over external paths as being parameterised by internal paths. We will call this a *variational density* (noting from 6 that internal paths are conditionally independent of external paths)	17

$\begin{aligned} \vec{\alpha} &= \arg\min_{\vec{\alpha}} L_{\bar{x}}\left(\vec{\alpha}\middle\vert\vec{s}\right) = \arg\min_{\vec{\alpha}} F\left(\vec{\alpha},\vec{s}\right) \\ &\Longrightarrow \nabla_{\vec{\alpha}} L\left(\vec{\alpha},\vec{s}\right) = 0 \\ &\Longrightarrow \nabla_{\vec{\alpha}} L\left(\vec{\alpha},\vec{s}\right) = \nabla_{\vec{\alpha}} \underbrace{D_{KL}\left[p_{\vec{\mu}}\left(\vec{\eta}\right) \Vert p_{\bar{x}}\left(\vec{\eta}\middle\vert\vec{s},\vec{\mathbf{a}}\right)\right]}_{\text{Divergence}=0} + \underbrace{\nabla_{\vec{\alpha}} L_{\bar{x}}\left(\vec{s},\vec{\alpha}\right)}_{=0} = 0 \end{aligned}$	The Lagrangian and variational free energy share the same minima, where their gradients vanish	18
$p_{\vec{\mu}}\left(\vec{\eta}\right)$	Density over external states parameterised by internal states	
$p_{\bar{x}}\left(\vec{\eta},\vec{\pi}\middle\vert x_0\right)$	a generative model encoded by their genotype	