

BIRTH-DEATH-MUTATION PROCESS WITH AN ENVIRONMENTAL PHENOTYPE

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Here, we consider a birth-death-mutation process in which each individual has an “internal” phenotype $x \in \mathcal{S}$, which is expressed as an “environmental” phenotype $\theta(x) \in \mathcal{E}$ that determines the vital rates of the individual. We assume that θ is one-to-one, but *not* onto.

We let $N(t)$ be the number of individuals at time t , and set $N(0) = n$ (n is the “system-size”, and *not* a fixed population size: $N(t)$ will vary stochastically with the birth and death events). We assume that some ordering is assigned to all individuals alive at time t (*e.g.*, we could order them by age) and let $X_i(t)$ be the phenotype of the i^{th} individual at time t . The population can then be represented by its empirical measure in $\mathcal{M}_P(\mathcal{S})$, the space of point measures on \mathcal{S}

$$\mu_t = \sum_{i=1} \delta_{X_i(t)}.$$

n.b., the empirical measure is independent of the ordering of the individuals, counting only the number of individuals of a given phenotype at time t . We can equally represent the population by the empirical measure of environmental phenotypes in $\mathcal{M}_P(\mathcal{E})$,

$$\theta_*(\mu_t) = \mu_t = \sum_{i=1} \delta_{\theta(X_i(t))}.$$

Here, $\theta_*(\mu_t)$ is the *pushforward* of μ_t by θ : more generally, given a measure $\mu \in \mathcal{M}(\mathcal{S})$, its pushforward is the measure $\theta_*(\mu) \in \mathcal{M}(\mathcal{E})$ defined by

$$\int_{\mathcal{E}} f d\theta_*(\mu) := \int_{\mathcal{S}} f \circ \theta d\mu.$$

In what follows, we will also make use of the *pullback* of functions $f \in C(\mathcal{E})$ by θ :

$$\theta^* f := f \circ \theta \in C(\mathcal{S}),$$

and the pullback of functions $F \in C(\mathcal{M}(\mathcal{E}))$ by θ_* : for $\mu \in \mathcal{M}(\mathcal{S})$,

$$\Theta^* F(\mu) := F(\theta_* \mu).$$

We assume that the birth and death rates of an individual, $b(\vartheta, \nu)$ and $d(\vartheta, \nu)$, respectively, depend on the *environmental* composition of the community, $\nu \in \mathcal{M}_P(\mathcal{E})$, but only on the *environmental* phenotype of the individual; an individual with internal type x has birth and death rates $b(\theta(x), \nu)$ and $d(\theta(x), \nu)$. Similarly, we assume (Lee?) that the probability that a new-born individual of type x carries a phenotype-changing mutation is $\varepsilon(\theta(x), \nu)$, whereas the probability that a parent of internal phenotype x gives birth to an offspring with internal phenotype y is given by the dispersal kernel $K(x, dy)$.

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With these, we can then describe the generator of the process, $\mathbb{L} : C(\mathcal{M}(\mathcal{S})) \rightarrow C(\mathcal{M}(\mathcal{S}))$,

$$(1) \quad \mathbb{L}F(\mu) = \int_{\mathcal{S}} \mu(dx) (1 - \varepsilon(\theta(x), \theta_*\mu)) b(\theta(x), \theta_*\mu) [F(\mu + \delta_x) - F(\mu)] \\ + d(\theta(x), \theta_*\mu) [F(\mu - \delta_x) - F(\mu)] \\ + \varepsilon(\theta(x), \theta_*\mu) b(\theta(x), \theta_*\mu) \int_{\mathcal{S}} K(x, dy) [F(\mu + \delta_y) - F(\mu)].$$

Alternately, we can consider the generator $\tilde{\mathbb{L}} : C(\mathcal{M}(\mathcal{E})) \rightarrow C(\mathcal{M}(\mathcal{E}))$ acting on the environmental phenotypes:

$$(2) \quad \tilde{\mathbb{L}}\Phi(\nu) = \int_{\mathcal{E}} \nu(d\vartheta) (1 - \varepsilon(\vartheta, \nu)) b(\vartheta, \nu) [\Phi(\nu + \delta_{\vartheta}) - \Phi(\nu)] \\ + d(\vartheta, \nu) [\Phi(\nu - \delta_{\vartheta}) - \Phi(\nu)] \\ + \varepsilon(\vartheta, \nu) b(\vartheta, \nu) \int_{\mathcal{E}} \theta_* K(\theta^{-1}(\vartheta), d\varsigma) [\Phi(\nu + \delta_{\varsigma}) - \Phi(\nu)].$$

Now, consider an internal phenotype process μ_t evolving according to (1), and the corresponding environmental phenotype process $\theta_*\mu_t$. The latter is characterized by knowing $\Phi(\theta_*\mu_t)$ for all $\Phi \in C(\mathcal{M}(\mathcal{E}))$. Now, $\Phi(\theta_*\mu_t) = \Theta^*\Phi(\mu_t) \in C(\mathcal{M}(\mathcal{S}))$, so we can in turn consider the action of (1) on $\Theta^*\Phi$:

$$\begin{aligned} \mathbb{L}(\Theta^*\Phi)(\mu) &= \int_{\mathcal{S}} \mu(dx) (1 - \varepsilon(\theta(x), \theta_*\mu)) b(\theta(x), \theta_*\mu) [\Theta^*\Phi(\mu + \delta_x) - \Theta^*\Phi(\mu)] \\ &\quad + d(\theta(x), \theta_*\mu) [\Theta^*\Phi(\mu - \delta_x) - \Theta^*\Phi(\mu)] \\ &\quad + \varepsilon(\theta(x), \theta_*\mu) b(\theta(x), \theta_*\mu) \int_{\mathcal{S}} K(x, dy) [\Theta^*\Phi(\mu + \delta_y) - \Theta^*\Phi(\mu)] \\ &= \int_{\mathcal{S}} \mu(dx) (1 - \varepsilon(\theta(x), \theta_*\mu)) b(\theta(x), \theta_*\mu) [\Phi(\theta_*\mu + \delta_{\theta(x)}) - \Phi(\theta_*\mu)] \\ &\quad + d(\theta(x), \theta_*\mu) [\Phi(\theta_*\mu - \delta_{\theta(x)}) - \Phi(\theta_*\mu)] \\ &\quad + \varepsilon(\theta(x), \theta_*\mu) b(\theta(x), \theta_*\mu) \int_{\mathcal{S}} K(x, dy) [\Phi(\theta_*\mu + \delta_{\theta(y)}) - \Phi(\theta_*\mu)] \\ &= \int_{\mathcal{E}} (\theta_*\mu)(d\vartheta) (1 - \varepsilon(\vartheta, \theta_*\mu)) b(\vartheta, \theta_*\mu) [\Phi(\theta_*\mu + \delta_{\vartheta}) - \Phi(\theta_*\mu)] \\ &\quad + d(\vartheta, \theta_*\mu) [\Phi(\theta_*\mu - \delta_{\vartheta}) - \Phi(\theta_*\mu)] \\ &\quad + \varepsilon(\vartheta, \theta_*\mu) b(\vartheta, \theta_*\mu) \int_{\mathcal{E}} \theta_* K(\theta^{-1}(\vartheta), d\varsigma) [\Phi(\theta_*\mu + \delta_{\varsigma}) - \Phi(\theta_*\mu)] \\ &= \tilde{\mathbb{L}}\Phi(\theta_*\mu) = \Theta^*(\tilde{\mathbb{L}}\Phi)(\mu), \end{aligned}$$

Giving the desired duality of generators.

To see the effect on selection, consider the case when $\Phi(\nu) = \langle \phi, \nu \rangle$ for some $\phi \in C(\mathcal{E})$ (recall that

$$\langle f, \mu \rangle = \int_{\mathcal{X}} f d\mu$$

when $f \in C(\mathcal{X})$ and $\mu \in \mathcal{M}(\mathcal{X})$. The previous calculations show us that

$$\begin{aligned} \frac{d}{dt} \mathbb{E}[\langle \phi, \theta_* \mu_t \rangle] &= \mathbb{E} \left[\int_{\mathcal{E}} (\theta_* \mu)(d\vartheta) ((1 - \varepsilon(\vartheta, \theta_* \mu_t))b(\vartheta, \theta_* \mu_t) - d(\vartheta, \theta_* \mu_t)) \phi(\vartheta) \right. \\ &\quad \left. + \varepsilon(\vartheta, \theta_* \mu_t)b(\vartheta, \theta_* \mu_t) \int_{\mathcal{E}} \theta_* K(\theta^{-1}(\vartheta), d\varsigma) \phi(\varsigma) \right] \\ &= \mathbb{E} [\langle ((1 - \varepsilon(\cdot, \theta_* \mu_t))b(\cdot, \theta_* \mu_t) - d(\cdot, \theta_* \mu_t)) \phi + \varepsilon(\cdot, \theta_* \mu_t)b(\cdot, \theta_* \mu_t) \langle \phi, \theta_* K(\theta^{-1}(\cdot)), \theta_* \mu_t \rangle \rangle] \\ &= \mathbb{E} [\langle \phi, ((1 - \varepsilon(\cdot, \theta_* \mu_t))b(\cdot, \theta_* \mu_t) - d(\cdot, \theta_* \mu_t)) \theta_* \mu_t + \langle \varepsilon(\cdot, \theta_* \mu_t)b(\cdot, \theta_* \mu_t) \theta_* K(\theta^{-1}(\cdot)), \theta_* \mu_t \rangle \rangle] \end{aligned}$$

Morally, this is giving us a PDE for $\theta_* \mu_t$:

$$\partial_t(\theta_* \mu_t) \text{ " = " } ((1 - \varepsilon(\cdot, \theta_* \mu_t))b(\cdot, \theta_* \mu_t) - d(\cdot, \theta_* \mu_t)) \theta_* \mu_t + \langle \varepsilon(\cdot, \theta_* \mu_t)b(\cdot, \theta_* \mu_t) \theta_* K(\theta^{-1}(\cdot)), \theta_* \mu_t \rangle$$

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