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THE PRINCIPLE OF PARTIAL CONTROL IN REACTION-DIFFUSION MODELS FOR THE EVOLUTION OF DISPERSAL

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Abstract. Studies using reaction-diffusion models for the evolution of dispersal have classified their behavior in terms of the categories of conditional vs. unconditional dispersal, and the operators of diffusion, nonlocal diffusion, advection, and spatial heterogeneity of growth rates. Recent results on resolvent positive operators reveal a different basis to classify their behavior: it focuses on the *form of variation* in the operators rather than the form of the operators themselves. When the variation consists of equal scaling of all dispersal and advection operators, selection favors reduced dispersal. But other forms of variation in the operators may select for increased dispersal. When variation has only partial control over the operators it may act effectively as though it were directed toward fitter habitats. The *principle of partial control* provides a heuristic for variation that favors increased dispersal. While some results for the classification of variation that produces departure from reduction have been obtained for finite matrices, the general classification problem remains open for both finite and infinite dimensional spaces.

1. **Introduction.**

A great deal of progress has been made recently in understanding the selective forces that shape the evolution of dispersal in heterogeneous environments over continuous space. Dispersal on continuous space is modeled by reaction-diffusion equations. The evolution of dispersal is analyzed in reaction-diffusion models by examining the fate of genetic variation for the dispersal operators. If we call the dispersal behavior of a population its *dispersal strategy*, then a fundamental question is what dispersal strategies may be evolutionarily stable. Evolutionary stability encompasses a number of mathematical properties, but fundamental among them is what happens to a small population with a different dispersal strategy when it is introduced into a population — does it go extinct or does it grow in size? This is the question of *invasibility*. What dispersal strategies can invade any given dispersal strategy? What dispersal strategies are or are not invadable?

The principal analytic task is to evaluate how the spectral radius of the dispersal operator changes as a function of variation in the operator. Analytic results for this question have been obtained for an ever-growing body of operators. Hastings [1] begins it with diffusion in a one-dimensional space having heterogeneous growth rates over the space, and zero quantity at the boundaries of the space (Dirichlet

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boundary conditions). Results were extended to zero-flux Neumann boundary conditions [2, Lemma 2.1],[3, Lemma 2.1][4]. Advection was added [5]. Results were obtained for nonlocal dispersal operators (kernel operators) [6]. Results have been obtained for mixtures of diffusion and nonlocal dispersal [7].

In a broad set of models, a reduction in the amount of dispersal increases the spectral radius of the operator, implying that variants having reduced dispersal will be able to invade populations whose residents have higher dispersal rates. These results are all concordant with the Reduction Principle from population genetics [8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 17, 20, 21, 22, 23], where reduced levels of recombination, mutation, and dispersal have been found to be selectively advantageous.

This similarity is not merely an analogy, but rather an underlying property of the interaction between mixing and growth. This is shown in [24], through an equivalence to a theorem of Kato [25], to follow.

2. **Theorems on Operator Variation.** Some terms must first be defined.

2.1. **Definitions.**

X represents an ordered Banach space or its complexification.

X_+ represents the proper, closed, positive cone of X, assumed to be generating and normal (see [25]).

$B(X)$ represents the set of all bounded linear operators $A\colon X \to X$.

$C(S)$ represents continuous functions on a compact Hausdorff space S.

A is a *positive operator* if $AX_+ \subset X_+$.

The resolvent of A is $R(\xi, A) := (\xi - A)^{-1}$, the operator inverse of $\xi - A$, $\xi \in \mathbb{C}$.

The resolvent set $\rho(A) \subset \mathbb{C}$ are those values of ξ for which $\xi - A$ is invertible.

The spectrum of $A \in B(X)$, $\sigma(A)$, is the complement of the resolvent set, $\rho(A)$.

The *spectral radius* of closed bounded linear operator A is

$$r(A) := \sup\{|\lambda|\colon \lambda \in \sigma(A)\}. \tag{1}$$

The *spectral bound* of closed linear operator A, not necessarily bounded, is

$$s(A) := \begin{cases} \sup\{\mathrm{Re}(\lambda)\colon \lambda \in \sigma(A)\} & \text{if } \sigma(A) \neq \emptyset \\ -\infty & \text{if } \sigma(A) = \emptyset. \end{cases}$$

The type (growth bound) of an infinitesimal generator, A, of a strongly continuous (C_0) semigroup, $\{e^{tA}\colon t > 0\}$, is

$$\omega(A) := \lim_{t\to\infty} \frac{1}{t} \log \|e^{tA}\| = \log r(e^A).$$

Resolvent positive operators are linear operators for which there is some $\xi_0 \in \mathbb{R}$ such that $(\xi_0, \infty) \subset \rho(A)$ and $R(\xi, A)$ is a positive operator for all $\xi > \xi_0$ [26].

2.2. **Two Equivalent Theorems.**

The two theorems discussed here give variational properties of the spectral bound of linear operators $\alpha A + \beta V$ with respect to variation in either $\alpha > 0$ or $\beta \in \mathbb{R}$, where A is a resolvent positive operator, and V is an operator of multiplication. Theorems 2.1 and 2.2 generalize finite matrix theorems of Cohen [27] and Karlin [28, Theorem 5.2], respectively, to linear operators on Banach spaces.

Theorem 2.1 (Kato [25])**.**

Consider $X = C(S)$ or $X = L^p(S)$, $l \leq p < \infty$, on a measure space S, or more generally, let X be the intersection of two L^p-spaces with different p's and different *weight functions. Let $A\colon X \to X$ be a linear operator which is resolvent positive. Let V be an operator of multiplication on X represented by a real-valued function v, where $v \in C(S)$ for $X = C(S)$, or $v \in L^\infty(S)$ for the other cases.*

Then $s(A+V)$ is a convex function of V. If in particular A is a generator of a C_0 semigroup, then both $s(A+V)$ and $\omega(A+V)$ are convex in V.

Theorem 2.2 (Altenberg [24])**.**
Let A be a resolvent positive linear operator, and V be an operator of multiplication, under the same assumptions as Theorem 2.1. Then for $\alpha > 0$,

1. *$s(\alpha\, A+V)$ is convex in α;*
2. *For each $\alpha > 0$, either*
   (a) *$s((\alpha+h)A+V) < s(\alpha\, A+V) + h\ s(A) \quad \forall\ h > 0$, or*
   (b) *$s((\alpha+h)A+V) = s(\alpha\, A+V) + h\ s(A) \quad \forall\ h > 0$;*
3. *In particular, when $s(A) = 0$ then $s(\alpha\, A+V)$ is non-increasing in α (the 'reduction phenomenon'), and when $s(A) < 0$ then $s(\alpha\, A+V)$ is strictly decreasing in α;*
4. *For each $\alpha > 0$,*

$$\frac{\mathrm{d}}{\mathrm{d}\alpha} s(\alpha\, A+V) \leq s(A), \tag{2}$$

except possibly at a countable number of points α, where the one-sided derivatives exist but differ:

$$\frac{\mathrm{d}}{\mathrm{d}\alpha_-} s(\alpha\, A+V) < \frac{\mathrm{d}}{\mathrm{d}\alpha_+} s(\alpha\, A+V) \leq s(A). \tag{3}$$

If A is a generator of a C_0-semigroup, then the above relations on $s(\alpha\, A+V)$ also apply to the type $\omega(\alpha\, A+V)$.

Theorems 2.1 and 2.2 are shown to be dual to each other by a *dual convexity* lemma:

Lemma 2.3 (Dual Convexity[24])**.** *Let $x \in \mathcal{D}_1 = (0,\infty)$ and $y \in \mathcal{D}_2 = [0,\infty)$. Let $f\colon \mathcal{D}_1 \times \mathcal{D}_2 \to \mathbb{R}$ have the following properties:*

$$f(\alpha x, \alpha y) = \alpha f(x,y), \ \text{for } \alpha > 0, \qquad \text{and} \tag{4}$$

$$f(x,y) \text{ is convex in } y. \tag{5}$$

Then:

1. *$f(x,y)$ is convex in x;*
2. *For each $x \in \mathcal{D}_1$, either*
   (a) *$f(x+h,y) < f(x,y) + h\, f(1,0)\ \forall\ h \in \mathcal{D}_1$; or*
   (b) *$f(x+h,y) = f(x,y) + h\, f(1,0)\ \forall\ h \in \mathcal{D}_1$.*
   For $y \neq 0$, if $f(x,y)$ is strictly convex in y, then $f(x,y)$ is strictly convex in x, and $f(x+h,y) < f(x,y) + h\, f(1,0)$.
3. *For each $x \in \mathcal{D}_1$,*

$$\frac{\partial}{\partial x} f(x,y) \leq f(1,0),$$

except possibly at a countable number of points x, where the one-sided derivatives exist but differ:

$$\frac{\partial}{\partial x_-} f(x,y) < \frac{\partial}{\partial x_+} f(x,y) \leq f(1,0).$$

The lemma holds if we substitute $\mathcal{D}_1 = (-\infty, 0)$ or $\mathcal{D}_2 = (-\infty, 0]$ or both.

Remark 2.4. It should be noted that the boundary conditions do not enter directly in either Theorem 2.1 or 2.2. In Theorem 2.1 boundary conditions enter only to the extent that they allow A to be the generator of a C_0 semigroup. In Theorem 2.2, they enter additionally in determining the value of $s(A)$ which is the upper bound for $\partial s(\alpha A + \beta V)/\partial\alpha$ (similarly $\omega(A)$). In particular:

1. when $s(A) = 0$ then $s(\alpha\, A + V)$ is convex non-increasing in α, and
2. when $s(A) < 0$ then $s(\alpha\, A + V)$ is strictly convex and strictly decreasing in α.

Diffusions with Dirichlet boundary conditions typically have $s(A) < 0$. Most of the models for the evolution of dispersal mentioned above [2, 3, 4, 5, 6, 7] assume reflecting Neumann boundary conditions, necessitating a refinement of Theorem 2.2 that gives conditions for a strict inequality $\partial s(\alpha A + V)/\partial\alpha < s(A)$. Work on this problem is ongoing.

2.3. **Implications of the Theorems.** A principle implication of Theorems 2.1 and 2.2 is that the details of the linear operator A are irrelevant to the variational behavior as long as A is resolvent positive. Theorem 2.2 shows that scaling of all parts of the operator besides the operator of multiplication, i.e. α in $L(\alpha) := \alpha A + V$, can only reduce or leave constant the spectral bound s or growth bound ω when $s(A) \leq 0$ or $\omega(A) \leq 0$, respectively. This is the *Reduction Principle* [15, 19, 24].

We know, therefore, that an increase in dispersal can increase the growth bound only if it has a form of variation different from $L(\alpha) = \alpha A + V$. With this perspective, we can re-examine the models in the literature in which increased dispersal increases the growth bound.

3. **Forms of Variation vs. Forms of Operators.** Here I collect examples from the literature in which operators in addition to the Laplacian, Δ, are analyzed. The usual setting is to examine the evolutionary stability of a dispersal pattern by competing two species that have different dispersal patterns. The functions $u(x)$ and $v(x)$ represent densities of the species at each spatial point x. Beginning with an equilibrium distribution $u(x,t)$ of a single species, a perturbation is made by introducing a small population of the competing species, $v(x,t)$. Throughout, $m(x)$ is an operator of multiplication that represents the population growth rate at each point x. The densities $u(x,t)$ and $v(x,t)$ themselves enter as operators of multiplication representing competition for growth resources between and within species. These quadratic terms in u and v are the density dependence that make the systems logistic rather than linear. The boundary conditions are in every case either Dirichlet or Neumann no-flux conditions, and are omitted here.

In the cases presented, varying α_i produces variation of the form $\alpha A + V$ from Theorem 2.2, and therefore the reduction principle applies, while varying the parameters $\nu, \mu, \gamma, \beta, \tau$ does not produce variation of the form $\alpha A + V$, and so it is possible for departures from reduction to occur. The time derivative is $u_t \equiv \partial u(x,t)/\partial t$.

3.0.1. *Belgacem and Cosner (1995)* [5]*, Cosner and Lou (2003)*[29].

$$u_t = \mu\Delta u - \beta\nabla m \cdot \nabla u + (m - cu)u \qquad \text{in } \Omega \times (0,\infty). \tag{6}$$

3.0.2. *Hambrock (2007)* [30] *, Chen, Hambrock, and Lou (2008)* [31]*, Lou (2008)* [32]*, Hambrock and Lou (2009)* [33].

$$u_t = \nabla \cdot [\mu\nabla u - \gamma u \nabla m] + u(m - u - v) \qquad \text{in } \Omega \times (0,\infty) \tag{7}$$

$$v_t = \nabla \cdot [\nu\nabla v - \beta v \nabla m] + v(m - u - v) \qquad \text{in } \Omega \times (0,\infty). \tag{8}$$

3.0.3. *Lou (2008)* [32].

$$u_t = \mu\Delta u + u(m(x) - u - [1 + \tau g(x)]v) \qquad \text{in } \Omega \times (0,\infty) \tag{9}$$

$$v_t = \mu\Delta v + v(m(x) - v - [1 + \tau h(x)]u) \qquad \text{in } \Omega \times (0,\infty). \tag{10}$$

Here, the variation is the change in the operator of multiplication, from $g(x)$ to $h(x)$. By Theorem 2.1, we know that the growth bound is convex in this variation.

3.0.4. *Bezugly (2009)* [34].

$$u_t = \alpha_1\nabla\cdot[\nabla u - \gamma u\nabla f(m)] + u(m - u - v) \qquad \text{in } \Omega \times (0,\infty) \tag{11}$$

$$v_t = \alpha_2\nabla\cdot[\nabla v - \beta v\nabla f(m)] + v(m - u - v) \qquad \text{in } \Omega \times (0,\infty). \tag{12}$$

where the function f is differentiable and $\mathrm{d}f(y)/\mathrm{d}y > 0$, $y \in [\min_\Omega m, max_\Omega m]$.

3.0.5. *Bezuglyy and Lou (2010)* [35].

$$u_t = \alpha_1\nabla\cdot[\nabla u - \gamma u\nabla m] + u(m - u - v) \qquad \text{in } \Omega \times (0,\infty) \tag{13}$$

$$v_t = \alpha_2\nabla\cdot[\nabla v - \beta v\nabla m] + v(m - u - v) \qquad \text{in } \Omega \times (0,\infty). \tag{14}$$

3.0.6. *Kao, Lou, and Shen (2012)* [7].

$$u_t = \alpha_1[\tau_1\Delta u + (1-\tau_1)Lu] + u(m - u - v) \qquad \text{in } (0,\infty)\times\mathbb{R}^N, \tag{15}$$

$$v_t = \alpha_2[\tau_2\Delta u + (1-\tau_2)Lv] + v(m - u - v) \qquad \text{in } (0,\infty)\times\mathbb{R}^N, \tag{16}$$

where L is a kernel operator

$$(Lu)(x) = \int_{\mathbb{R}^N} K(|x-y|)\; u(y)\; \mathrm{d}y - u(x),$$

$K(r)\colon [0,\infty) \to [0,\infty)$ is smooth, monotone decreasing and has compact support, the system is spatially periodic, $u(t,x+p) = u(t,x), v(t,x+p) = v(t,x), (t,x) \in (0,\infty)\times\mathbb{R}^N$, and habitat quality $a(x)$ is non-constant, positive and p-periodic in $\mathbb{R}^N$.

The biological situations modeled in the dispersal literature have covered only a small sampling of the space of resolvent positive operators covered under Theorem 2.2. The Laplace operator can be generalized to second-order elliptic operators on $L^p(\Omega)$ of the form

$$A = -\sum_{j,k=1}^{N} \frac{\partial}{\partial x_k}\left(a_{jk}\frac{\partial}{\partial x_j}\right) + \sum_{j=1}^{N} b_j\frac{\partial}{\partial x_j} + \frac{\partial}{\partial x_j}(c_j.) + a_0,$$

with all the appropriate assumptions [36]. Elliptic operators can be combined with kernel operators to yield new resolvent positive operators. As long as variation is of the form $\alpha A + V$, the reduction principle will apply.

4. **Departures from Reduction.** In the studies cited above, variation that is not of the form $\alpha A + V$ has required detailed analysis of the particulars of the operators to know how the growth bound changes with the variation in the operator. The key open problem is to provide a general classification of the variation that produces departures from reduction. Let A and B be operators on a Banach space such that $\alpha A + \beta B$ is resolvent positive for $\alpha > 0$, $\beta \geq 0$. The problem may be stated as finding necessary or sufficient conditions on operators B such that

$$\frac{\partial}{\partial\alpha} s(\alpha A + \beta B) > s(A).$$

A necessary condition, by dual convexity and Theorem 2.2, is that $s(\alpha A+\beta B)$ *not* be convex for all $\beta > 0$ (see Theorem 4.1). A sufficient condition, by dual convexity, is that $s(\alpha A+\beta B)$ be concave for all $\beta > 0$. This is presented formally as follows.

Theorem 4.1 (Contrapositive to Lemma 2.3)**.**
Let $x \in \mathcal{D}_1 = (0, \infty)$ and $y \in \mathcal{D}_2 = [0, \infty)$. Let $f \colon \mathcal{D}_1 \times \mathcal{D}_2 \to \mathbb{R}$ be homogeneous of order one:

$$f(\alpha x, \alpha y) = \alpha f(x, y), \ \text{for } \alpha > 0. \tag{17}$$

If there exist $x_1, y_1 > 0$ such that

$$\left. \frac{\partial f(x, y_1)}{\partial x} \right|_{x=x_1} > f(1, 0), \tag{18}$$

then $f(x, y)$ is strictly concave in y somewhere on $y \in \big(0, \dfrac{xy_1}{x_1}\big) \subset \mathcal{D}_2$, for each $x \in \mathcal{D}_1$.

Proof. Let $s > 0$ and

$$\left. \frac{\partial f(x, y_1)}{\partial x} \right|_{x=x_1} = f(1, 0) + s. \tag{19}$$

By the definition of the derivative [37, Definitions 4.1, 5.1], (18) requires that for every $\epsilon > 0$ there exists a $\delta > 0$ such that

$$\left| \frac{f(x_1 + h, y_1) - f(x_1, y_1)}{h} - (f(1, 0) + s) \right| < \epsilon$$

for all $h \in (-\delta, \delta)$. This is equivalent to

$$-\epsilon < \frac{f(x_1 + h, y_1) - f(x_1, y_1)}{h} - (f(1, 0) + s) < \epsilon,$$

and if we set $0 < h < \delta$, this is equivalent to the conjunction of

$$(s - \epsilon)h < f(x_1 + h, y_1) - f(x_1, y_1) - hf(1, 0) < (\epsilon + s)h \tag{20}$$

and

$$(s - \epsilon)h < f(x_1, y_1) - f(x_1 - h, y_1) - hf(1, 0) < (\epsilon + s)h. \tag{21}$$

Application of the homomorphism (17) shows (20) to be equivalent to:

$$\frac{(s - \epsilon)h}{x_1 + h} < f\left(1, \frac{y_1}{x_1 + h}\right) - \frac{x_1}{x_1 + h} f\left(1, \frac{y_1}{x_1}\right) - \frac{h}{x_1 + h} f(1, 0) < \frac{(\epsilon + s)h}{x_1 + h},$$

and shows (21) to be equivalent to:

$$\frac{(s - \epsilon)h}{x_1} < f\left(1, \frac{y_1}{x_1}\right) - \frac{x_1 - h}{x_1} f\left(1, \frac{y_1}{x_1 - h}\right) - \frac{h}{x_1} f(1, 0) < \frac{(\epsilon + s)h}{x_1}.$$

We consider $\epsilon \in (0, s)$ so $s - \epsilon > 0$. Then for all $0 < h < \delta$, after rearranging and homogenous multiplication by $x > 0$, we get

$$f\left(x, \frac{xy_1}{x_1 + h}\right) > \frac{x_1}{x_1 + h} f\left(x, \frac{xy_1}{x_1}\right) + \frac{h}{x_1 + h} f(x, 0), \tag{22}$$

and

$$f\left(x, \frac{xy_1}{x_1}\right) > \frac{x_1 - h}{x_1} f\left(x, \frac{xy_1}{x_1 - h}\right) + \frac{h}{x_1} f(x, 0). \tag{23}$$

The second arguments of $f(\cdot,\cdot)$ in (22) and (23) are related by convex combination:

$$\frac{xy_1}{x_1+h} = \frac{x_1}{x_1+h}\,\frac{xy_1}{x_1} + \frac{h}{x+h} * 0, \text{ and } \frac{xy_1}{x_1} = \frac{x_1-h}{x_1}\,\frac{xy_1}{x_1-h} + \frac{h}{x_1} * 0.$$

Thus (22) and (23) are concavity inequalities, and therefore (20) and (21) and (18) require concavity in y of $f(x,y)$ somewhere in the interval $y \in \big(0, \frac{xy_1}{x_1}\big) \subset \big(0, \frac{xy_1}{x_1-h}\big)$ (the larger interval is superfluous to the theorem).

If concavity is replaced by convexity and the direction of inequality in (17) is reversed, one obtains a convexity version of the theorem. □

Remark 4.2. The converse of Theorem 4.1 is not true; i.e. concavity somewhere in $y \in (0, xy_1/x_1)$ is not sufficient to imply $\partial f(x,y_1)/\partial x\big|_{x=x_1} > f(1,0)$. But concavity in all $\beta > 0$ is clearly is sufficient, being the concave version of of Lemma 2.3 (see Corollary 4.4).

Corollary 4.3 (Concavity Necessary for Departures from Reduction)**.** *Let $\alpha A+\beta B$ be a family of resolvent positive operators, with $\alpha > 0$ and $\beta \geq 0$. Suppose there exist α_1 and β_1 such that*

$$\left.\frac{\partial s(\alpha A + \beta_1 B)}{\partial \alpha}\right|_{\alpha=\alpha_1} > s(A). \tag{24}$$

Then $s(\alpha A + \beta B)$ is strictly concave in β somewhere on $\beta \in \big(0, \frac{\alpha\beta_1}{\alpha_1}\big)$, for each $\alpha > 0$.

Proof. This follows directly from Theorem 4.1 and does not depend on any property of the spectral bound beyond homogeneity of degree one. □

Corollary 4.4 (Sufficient Concavity for Departures from Reduction)**.** *Let $\alpha A+\beta B$ be a family of resolvent positive operators, with $\alpha > 0$ and $\beta \geq 0$. If $s(\alpha A + \beta B)$ is concave in β for all $\beta > 0$, then*

$$\frac{\partial s(\alpha A + \beta B)}{\partial \alpha} \geq s(A). \tag{25}$$

Proof. This follows directly from the concave version of Lemma 2.3 and does not depend on any property of the spectral bound beyond homogeneity of degree one, and so is true for all such homogeneous functions. □

Remark 4.5. Kato [25] gives an example to which Corollary 4.4 is applicable: Let $X = L^p(0,1)$, $u \in X$, with boundary conditions $u(0) = u(1) = 0$. Let $A = d^2/dx^2$, and $B = -d/dx$. Then A and B are semigroup-positive and resolvent positive by [25, Lemma 5.1], and for $\alpha, \beta > 0$, $s(\alpha A+\beta B) = -\pi^2\alpha - \beta^2/4\alpha$. Clearly $s(\alpha A+\beta B)$ is concave in both α and β. Hence $\partial s(\alpha A+\beta B)/\partial\alpha \geq s(A)$ by Corollary 4.4, which is confirmed by evaluation: $\beta^2/(4\alpha^2) - \pi^2 \geq -\pi^2$.

With respect to biological phenomena, there are two principle causes why variation in operators may not be of the form $\alpha A + V$:

Multiple operators. There may be multiple, *independently varied* operators acting on a quantity. In the case of dispersal, we have seen diffusion with independent advection as an example [5];

Directed variation. The variation may not scale the mixing process uniformly. In the case of dispersal, the primary example is conditional dispersal [30, 33].

Out of these observations come two heuristics for how multiple processes may produce departures from reduction:

Principle 1 (The principle of partial control [19])**.** When variation has only partial control over the transformations occurring on types under selection, then it may be possible for the part which it controls to evolve an increase in rates.

Principle 2 (Partial Control and Induced Directed Variation [38])**.** Undirected variation of a transformation process, i.e. equal scaling of all transition probabilities by a rate m, may act effectively like *directed* variation toward fitter types due to dynamics induced by other transformation processes and selection, so that increases in m increase the population growth rate ρ.

The classification of variation that produces departures from reduction is an open question for resolvent positive operators on infinite dimensional Banach spaces. For operators on finite vector spaces, however, some progress has been made toward a classification. The following recent result gives the relationship between the eigenvalues of the operators and the reduction phenomenon.

Theorem 4.6 (Departure from Reduction [38])**.**
Let $\mathbf{P}$ and $\mathbf{Q} \in \mathbb{R}^{n,n}$ be transition matrices of reversible ergodic Markov chains that commute with each other. Let $\mathbf{D} \neq c\,\mathbf{I}$ be a positive diagonal matrix, and

$$\mathbf{M}(m) := \mathbf{P}[(1{-}m)\mathbf{I} + m\mathbf{Q}], \qquad m \in [0,1]. \tag{26}$$

1. *If all eigenvalues of $\mathbf{P}$ are positive, then the reduction phenomenon holds:*
$$\frac{\mathrm{d}}{\mathrm{d}m}\rho(\mathbf{M}(m)\mathbf{D}) < 0. \tag{27}$$
2. *If all eigenvalues of $\mathbf{P}$ other than $\lambda_1(\mathbf{P}) = 1$ are negative, then departure from the reduction phenomenon is found:*
$$\frac{\mathrm{d}}{\mathrm{d}m}\rho(\mathbf{M}(m)\mathbf{D}) > 0. \tag{28}$$

A special case of Theorem 4.6 is the following, derived for a model of multilocus mutation. The condition $\mu_\xi < 1/2$ ensures that all the eigenvalues positive, making Theorem 4.6 item 1 applicable.

Theorem 4.7 (Multivariate, Multiplicative Variation [39])**.** *Consider the stochastic matrix*

$$\mathbf{M}_{\boldsymbol{\mu}} := \bigotimes_{\xi=1}^{L} \left[(1-\mu_\xi)\mathbf{I}^{(\xi)} + \mu_\xi \mathbf{P}^{(\xi)}\right], \tag{29}$$

where $L \geq 2$, $\boldsymbol{\mu} \in (0,1/2)^L$, each of the matrices $\mathbf{P}^{(\xi)}$ is a $n_\xi \times n_\xi$ transition matrix for a reversible ergodic Markov chain, $\bigotimes$ is their Kronecker (tensor) product, and $0 < \mu_\xi < 1/2$. Let $\mathbf{D} \neq c\mathbf{I}$ be a positive diagonal matrix of order $N \times N$, where $N := \prod_{\xi=1}^{L} n_\xi$.

Then for every point $\boldsymbol{\mu} \in (0,1/2)^L$, the spectral radius of

$$\mathbf{M}_{\boldsymbol{\mu}}\mathbf{D} = \left\{ \bigotimes_{\xi=1}^{L} \left[(1-\mu_\xi)\mathbf{I}^{(\xi)} + \mu_\xi \mathbf{P}^{(\xi)}\right] \right\} \mathbf{D}$$

is non-increasing in each μ_ξ.

The reversible Markov chain condition is made so that the Rayleigh-Ritz variational formula for the spectral radius may be employed. Analogous variational principles apply to classes of operators on Banach spaces. It is most certain that Banach space versions of Theorems 4.6 and 4.7 can be obtained.

The complete classification problem, however, remains open for both finite matrices and operators on Banach spaces.

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