

Contrasts for a within-species comparative method

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Abstract

If we ask how we can construct a within-species counterpart to comparative methods that are used to correct for effects of phylogeny in between-species comparisons, we find that migration matrices, not phylogenies, are the relevant structures. Just as the hierarchical pattern of relatedness between species leads to a set of contrasts that are independent, the spectrum of the migration matrix leads to contrasts between population. If these contrasts are not used, migration can cause an artifactual appearance of a correlation between a phenotype and an environmental variable. The contrasts are derived from the spectral analysis of the migration matrix, and it is shown how to transform means and covariances between populations into variables that can be assumed independent, eliminating the artifact.

8.1 Introduction

When a quantitative character is measured in multiple populations of a geographically differentiated species, it is interesting to compare the values with those of environmental variables or of other characters. If a correlation is seen, it is tempting to test it statistically, using the mean values in different populations as independent points. The difficulty with doing this is that gene flow can cause nearby points to be correlated. If two populations are neighbors, and one happens to have attained a large value of the character by genetic drift, the other may have a similar value as a result of the gene flow between them. The similar values in the two populations should not be taken as evidence of response to a local environmental variable.

A similar issue arises between species, where individual species in a phylogeny should not be taken as independent data points. Their shared ancestry plays a role similar to gene flow. Harvey and Pagel (1991) have reviewed the issues and their proposed solutions for the between-species case. The most widely-used method to correct for the phylogeny in between-species analyses has been the contrasts method (Felsenstein, 1985), which uses the phylogeny to set up between-species contrasts that are independent. These can form the basis for a statistical analysis that escapes the problem of phylogenetic nonindependence.

Can a similar approach be used in the within-species case? The issues are quite similar. It is tempting to use molecular sequences to infer a “phylogeny” within the species and then to form contrasts based on that. This temptation should be resisted. The phylogeny would reflect the coalescent genealogy of that particular locus; a different locus is expected to show a different coalescent. If populations have been exchanging migrants for a long time, there is no reason to assume that there is an underlying treelike genealogy.

In this paper, I will use a simple model of genetic drift, migration and selection to describe the evolution of a phenotype, and to see whether contrasts can be found which solve the problem of nonindependence of populations owing to gene flow. Such contrasts are found, though they bear no close relationship to the contrasts used between species. The methods are consistent with those used by Hansen et. al. (2000), who correct for autocorrelation between neighboring populations in an analysis of spatial variation of characters. In effect, the present analysis generalizes their approach to arbitrary migration matrices. It is less easy to see how the present analysis relates to the autocorrelation methods used by Edwards and Kot (1995).

8.2 The model

The model is close to that of Lande (1976). It assumes that a quantitative character evolves on an infinitely long scale. We follow the mean phenotype x_i in each population. The genetics of the trait is not modelled explicitly; it is assumed that the heritability of the trait is constant. Natural selection in population i causes the mean phenotype to move a fraction σ of the way towards the local optimum phenotype p_i . Gene flow causes the mean phenotypes of different populations to be averaged, with the migration rate from population j to population i being m_{ij} . This quantity is then also the weight of x_j in the mean phenotype of population i in the next generation.

Note that the heritability of the character is implicit in the quantity σ , which is affected both by the heritability and by the strength of the optimum selection. The rule used here is the one which would result from selection with a Gaussian fitness function, constant additive genetic variance, and constant environmental variance in the character.

Genetic drift causes the mean phenotype in population i to change by a random amount ε_i , which is drawn from a normal distribution with mean 0 and variance β/N_i . The N_i are the sizes of the populations, and these do not change. The life cycle consists of migration, followed by selection, followed by random sampling for genetic drift.

The result of these assumptions is a simple autoregressive moving average process. In vector notation (boldfaced letters are vectors, boldfaced capital letters are matrices)

$$\mathbf{x}^{(t+1)} = \sigma \mathbf{p} + (1 - \sigma) \mathbf{M} \mathbf{x}^{(t)} + \boldsymbol{\varepsilon} \quad (1)$$

This will lead \mathbf{x} to be drawn from a multivariate normal distribution. We assume that we have observed the phenotype in the present generation, and that enough time has elapsed that the system has reached its equilibrium distribution.

8.3 The expectations of the phenotypes

Taking expectations of all terms in equation (1), we note that all quantities are constant except for the random variable \mathbf{x} , so that

$$\mathbb{E}[\mathbf{x}] = \sigma \mathbf{p} + (1 - \sigma) \mathbf{M} \mathbb{E}[\mathbf{x}] \quad (2)$$

which is easily solved to give

$$\mathbb{E}[\mathbf{x}] = (\mathbf{I} - (1 - \sigma)\mathbf{M})^{-1} \sigma \mathbf{p} \quad (3)$$

Thus the phenotypes will reflect the local optimum values p_i , but smoothed by the migration among populations.

8.4 Covariances of means between populations

If we take the equation (1), and subtract from it the expectations (3): we find that if $\mathbf{y} = \mathbf{x} - \mathbb{E}[\mathbf{x}]$,

$$\mathbf{y}^{(t+1)} = (1 - \sigma) \mathbf{M} \mathbf{y}^{(t)} + \boldsymbol{\varepsilon}. \quad (4)$$

Since the matrix of covariances of populations is given by

$$\mathbf{C} = \mathbb{E}[\mathbf{y}\mathbf{y}^T] \quad (5)$$

we end up with the equation

$$\mathbf{C} = (1 - \sigma)^2 \mathbf{M} \mathbf{C} \mathbf{M}^T + \mathbf{V}, \quad (6)$$

where \mathbf{V} is the covariance matrix of the changes $\boldsymbol{\varepsilon}$ due to drift, which will be a diagonal matrix as drift operates independently in different populations. In fact, the variance due to drift will be inversely proportional to the effective population size, so that if \mathbf{D} is a diagonal matrix of population sizes, whose i -th diagonal element is N_i ,

$$\mathbf{V} = \beta \mathbf{D}^{-1}. \quad (7)$$

8.5 Statistical tasks

Let us assume that the biologist has an estimate of either the relative or the absolute rates of migration between populations. Although much of the evolutionary literature centers on estimation of overall measures of divergence such as F_{ST} , coalescent likelihood methods (Bahlo and Griffiths, 2000; Beerli and Felsenstein, 2001) now permit estimation of the full set of migration rates using molecular data. These estimates are usually not the migration rates m_{ij} themselves, but are scaled by the effective population sizes so that they are the $N_i m_{ij}$

Suppose that we want to compare the mean phenotypes of the populations, collected at one time, to environmental variables measured in the populations, to test the hypothesis that the optimum phenotype is correlated with these environmental variables. Migration among populations leaves us uncertain whether similarities among populations are due to similarities of optimum phenotype or similarities due to gene flow. Figure 1 is an example of the problem. It appears to show a definite trend in phenotype along a chain of 20 populations. Actually, it is the result of a computer simulation in which the expected mean phenotype is the same in all populations. The migration structure is a linear stepping-stone chain of populations with $m_{i,i+1} = m_{i,i-1} = 0.1$, $\beta = 0.01$ and $\sigma = 0.01$. The optimum phenotype is 3 in all populations.

The apparent trend is a fortuitous result of correlation of neighboring populations by gene flow. This phenomenon has been noted by Kimura and Maruyama (1971), who found that with the appropriate amount of gene flow the pattern of gene frequencies in an array of populations “mimics a cline formed by selection”.

To avoid the effects of gene flow and selection being confounded, we need to make comparisons in which similarity of natural selection does not exactly mimic similarity due to gene flow. We must correct for the pattern of similarity due to gene flow in order to see similarities due to natural selection. To the extent that the patterns of similarity of environments differ from those expected due to gene flow, we can test for the effect of natural selection.

The joint distribution of phenotypic means of populations will be multivariate normal. It can therefore be characterized completely by the expectations of the means of the populations and the covariances among them.

8.6 Spectrum of the migration matrix

The eigenvalues and eigenvectors of the migration matrix will be central to the derivations, so we will start by obtaining them. Similar Fourier transform methods have been widely used in analyzing the expected patterns of genetic differentiation when there is a balance between migration and genetic drift (e.g. Malécot, 1948).

We have assumed that m_{ij} is the fraction of newborns in population i that are newly arrived from population j . N_i is the population number of population i . Assume that migration is *conservative*, i.e. that there is “detailed balance” between migrants into and out of each population. This means that the rates of migration between every pair of populations is set so that

$$N_i m_{ij} = N_j m_{ji}, \quad (8)$$

This has the effect that the numbers of migrants F_{ij} between i and j each generation are equal in the two directions, so that the matrix \mathbf{F} is symmetric.

Recalling that \mathbf{D} is the diagonal matrix of the N_i ,

$$\mathbf{M} = \mathbf{D}^{-1} \mathbf{F} \quad (9)$$

and if we premultiply by $\mathbf{D}^{1/2}$ and postmultiply by $\mathbf{D}^{-1/2}$ we get

$$\mathbf{D}^{1/2} \mathbf{M} \mathbf{D}^{-1/2} = \mathbf{D}^{-1/2} \mathbf{F} \mathbf{D}^{-1/2} = \mathbf{H}. \quad (10)$$

This matrix \mathbf{H} is symmetric since \mathbf{F} is symmetric. We can rewrite it as

$$\mathbf{H} = \mathbf{I} + \alpha \mathbf{G}. \quad (11)$$

where \mathbf{G} is symmetric. As \mathbf{G} is defined using the “fudge-factor” α we can think of it as indicating *relative* rates of migration (adjusted for population sizes).

Suppose that the spectral decomposition of the symmetric matrix \mathbf{G} is

$$\mathbf{G} = \mathbf{U} \mathbf{\Lambda} \mathbf{U}^T \quad (12)$$

Using this, the spectral decomposition of \mathbf{H} is

$$\mathbf{H} = \mathbf{U} (\mathbf{I} + \alpha\mathbf{\Lambda}) \mathbf{U}^T \quad (13)$$

and since

$$\mathbf{U}^T \mathbf{D}^{1/2} = (\mathbf{D}^{-1/2} \mathbf{U})^{-1}, \quad (14)$$

using (13) and (10), the spectral decomposition of \mathbf{M} is

$$\mathbf{M} = (\mathbf{D}^{-1/2} \mathbf{U}) (\mathbf{I} + \alpha\mathbf{\Lambda}) (\mathbf{D}^{-1/2}\mathbf{U})^{-1}. \quad (15)$$

8.7 The spectrum of the means

We already have the expectations of the mean phenotypes. The transformation $(\mathbf{D}^{-1/2}\mathbf{U})^{-1}$ leads to a particularly nice and useful expression. From (15) we can write the spectral decomposition of $\mathbf{I} - (1 - \sigma)\mathbf{M}$ as:

$$\mathbf{I} - (1 - \sigma)\mathbf{M} = (\mathbf{D}^{-1/2}\mathbf{U}) (\mathbf{I} - (1 - \sigma)(\mathbf{I} + \alpha\mathbf{\Lambda})) (\mathbf{D}^{-1/2}\mathbf{U})^{-1}. \quad (16)$$

and its inverse is then

$$(\mathbf{I} - (1 - \sigma)\mathbf{M})^{-1} = (\mathbf{D}^{-1/2}\mathbf{U}) (\mathbf{I} - (1 - \sigma)(\mathbf{I} + \alpha\mathbf{\Lambda}))^{-1} (\mathbf{D}^{-1/2}\mathbf{U})^{-1}. \quad (17)$$

and using (3) that leads to a form for the expectations of the phenotypes:

$$(\mathbf{D}^{-1/2}\mathbf{U})^{-1} \mathbb{E}[\mathbf{x}] = (\mathbf{I} - (1 - \sigma)(\mathbf{I} + \alpha\mathbf{\Lambda}))^{-1} (\mathbf{D}^{-1/2}\mathbf{U})^{-1} \sigma\mathbf{p} \quad (18)$$

The upshot of this is that the expectations of \mathbf{x} , if they are transformed by being multiplied by the transformation $(\mathbf{D}^{-1/2}\mathbf{U})^{-1}$ (which is the one that diagonalizes \mathbf{M}), are simply multiples of the corresponding transform of the optima \mathbf{p} . Thus, in effect, migration damps the spectrum of \mathbf{p} by multiplying its i -th element by

$$\frac{\sigma}{1 - (1 - \sigma)(1 + \alpha\lambda_i)} \quad (19)$$

(the eigenvalues λ_i are negative so this actually *is* a dampening).

8.8 The spectrum of the covariances

If we take the equation (6) and apply the same transformation $(\mathbf{D}^{-1/2}\mathbf{U})^{-1}$, we find that

$$\begin{aligned} \text{Cov}[(\mathbf{D}^{-1/2}\mathbf{U})^{-1} \mathbf{y}] &= (\mathbf{D}^{-1/2}\mathbf{U})^{-1} \mathbf{C} ((\mathbf{D}^{-1/2}\mathbf{U})^{-1})^T \\ &= (1 - \sigma)^2 (\mathbf{D}^{-1/2}\mathbf{U})^{-1} \mathbf{M} \mathbf{C} \mathbf{M}^T ((\mathbf{D}^{-1/2}\mathbf{U})^{-1})^T \\ &\quad + (\mathbf{D}^{-1/2}\mathbf{U})^{-1} \mathbf{V} ((\mathbf{D}^{-1/2}\mathbf{U})^{-1})^T \end{aligned} \quad (20)$$

Given the spectral decomposition of \mathbf{M} from (15), If we define the \mathbf{B} as the covariances of the transformed means

$$\mathbf{B} = \text{Cov}[(\mathbf{D}^{-1/2}\mathbf{U})^{-1} \mathbf{y}] \quad (21)$$

then we see, using equation (7)

$$\mathbf{B} = (1 - \sigma)^2 (\mathbf{I} + \alpha\mathbf{\Lambda}) \mathbf{B} (\mathbf{I} + \alpha\mathbf{\Lambda}) + \beta\mathbf{I}. \quad (22)$$

Setting up separate equations for each of the b_{ij} and solving them, we can readily show that the off-diagonal elements are all zero, so that the solution is the diagonal matrix

$$\mathbf{B} = \beta (\mathbf{I} - (1 - \sigma)^2(\mathbf{I} + \alpha\mathbf{\Lambda})^2)^{-1} \quad (23)$$

Thus transforming the phenotype to new values z_i by multiplying their values by the matrix $(\mathbf{D}^{-1/2}\mathbf{U})^{-1}$ creates a set of values that are independent. They have zero covariances and the variance of the i -th value is

$$\text{Var}[z_i] = \frac{\beta}{1 - (1 - \sigma)^2(1 + \alpha\lambda_i)^2} \quad (24)$$

Knowing the matrix \mathbf{B} we could easily undo the transformation and obtain \mathbf{C} :

$$\begin{aligned} \mathbf{C} &= (\mathbf{D}^{-1/2}\mathbf{U}) \mathbf{B} (\mathbf{D}^{-1/2}\mathbf{U})^T \\ &= (\mathbf{D}^{-1/2}\mathbf{U}) \beta (\mathbf{I} - (1 - \sigma)^2(\mathbf{I} + \alpha\mathbf{\Lambda})^2)^{-1} (\mathbf{D}^{-1/2}\mathbf{U})^T \end{aligned} \quad (25)$$

However we will use the expectations and variances of the transformed values instead.

8.9 Fitting models to the means

With n populations, with means from each, and an environmental variable or variables such as temperature τ , we can imagine fitting a model for the optima \mathbf{p} :

$$p_i = a + b\tau_i \quad (26)$$

In this case we have variables α , β , σ , a , and b . With n populations we can fit these and have $n - 5$ degrees of freedom left over. We can imagine doing likelihood ratio tests of hypotheses such as $b = 0$ or $\sigma = 0$.

We can also imagine knowing α , which makes for one more degree of freedom.

The likelihood ratio test could be done in either of two equivalent ways. With the original phenotypic means \mathbf{x} we could, for each possible set of parameter values, compute the expectations $\mathbb{E}[\mathbf{x}]$ from equation (3) and their covariances $\mathbf{C} = \text{Cov}[\mathbf{x}]$ from equation (25), and compute the likelihood from the usual multivariate normal density. The likelihood ratio test of dependence of the phenotypic means on the temperature τ would be a test of whether $b = 0$.

Alternatively, we could use the transformation $(\mathbf{D}^{-1/2}\mathbf{U})^{-1}$ on the vector x to make the values in the resulting vector \mathbf{z} independent. Then

1. Apply the transform to a vector of 1's. This will result in a vector with one nonzero element. Call this vector \mathbf{v} .
2. Apply the same transform to the vector $\boldsymbol{\tau}$. Call the resulting vector \mathbf{w} .
3. The expectation of z_i is $\sigma(a v_i + b w_i)/(1 - (1 - \sigma)(1 + \alpha\lambda_i))$
4. The variance of z_i is $\beta/(1 - (1 - \sigma)^2(1 + \alpha\lambda_i)^2)$

The z_i are independently normally distributed. From the z_i and their expectations and variances we can compute the likelihood as a product of these univariate normal densities. It might be thought necessary to take the Jacobian of the transformation into account. It involves only the population sizes N_i . As these do not depend on any of the parameters being estimated, its absence does not alter their estimated values, and it disappears from the likelihood ratio calculation.

Doing the test this way has considerable advantages. a and b can be estimated from a simple regression, and the absence of covariances among the z_i simplifies the expressions.

Alternatively, one could imagine exploratory approaches that first transform the mean phenotypes, then restandardize each value z_i to have expected mean 0 and variance 1. Exploratory statistical methods could then be used to see whether there is any noticeable trend in these values, and they could be compared to analogous transformations of environmental variables.

8.10 An example

Figure 2 shows the migration pattern for 5 populations, assumed to be equal in size. Migration is assumed symmetric in this simple case. The migration matrix is

$$\begin{bmatrix} 0.945 & 0.03 & 0 & 0 & 0.025 \\ 0.03 & 0.905 & 0 & 0.04 & 0.025 \\ 0 & 0 & 0.945 & 0.03 & 0.025 \\ 0 & 0.04 & 0.03 & 0.905 & 0.025 \\ 0.025 & 0.025 & 0.025 & 0.025 & 0.9 \end{bmatrix}$$

This corresponds to $\alpha = 0.1$ with the \mathbf{G} matrix

$$\mathbf{G} = \begin{bmatrix} -0.55 & 0.3 & 0 & 0 & 0.25 \\ 0.3 & -0.95 & 0 & 0.4 & 0.25 \\ 0 & 0 & -0.55 & 0.3 & 0.25 \\ 0 & 0.4 & 0.3 & -0.95 & 0.25 \\ 0.25 & 0.25 & 0.25 & 0.25 & -1 \end{bmatrix}$$

The spectral analysis of G is:

$$\begin{aligned}
\mathbf{G} &= \mathbf{U} \mathbf{\Lambda} \mathbf{U}^t \\
&= \begin{bmatrix} 0.223607 & -0.223607 & 0.5 & 0.67082 & 0.447214 \\ -0.67082 & -0.223607 & -0.5 & 0.223607 & 0.447214 \\ -0.223607 & -0.223607 & 0.5 & -0.67082 & 0.447214 \\ 0.67082 & -0.223607 & -0.5 & -0.223607 & 0.447214 \\ 0 & 0.894427 & 0 & 0 & 0.447214 \end{bmatrix} \\
&\quad \times \begin{bmatrix} -1.45 & 0 & 0 & 0 & 0 \\ 0 & -1.25 & 0 & 0 & 0 \\ 0 & 0 & -0.85 & 0 & 0 \\ 0 & 0 & 0 & -0.45 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix} \\
&\quad \times \begin{bmatrix} 0.223607 & -0.67082 & -0.223607 & 0.67082 & 0 \\ -0.223607 & -0.223607 & -0.223607 & -0.223607 & 0.894427 \\ 0.5 & -0.5 & 0.5 & -0.5 & 0 \\ 0.67082 & 0.223607 & -0.67082 & -0.223607 & 0 \\ 0.447214 & 0.447214 & 0.447214 & 0.447214 & 0.447214 \end{bmatrix}
\end{aligned}$$

With population sizes being equal, the rows of the matrix \mathbf{U}^T are the coefficients of the coordinates of the new transformation. Four of them represent contrasts between populations. These are shown roughly in Figure 3. They include left versus right, top versus bottom, one diagonal versus the other, and outside versus inside. The other coordinate is simply an average value that weights all populations equally.

Figure 4 shows the contrasts for the case of Figure 1, each expressed as a standardized deviation from its expectation, for the same data set. There is no noticeable departure from independent normal distribution of the contrast scores. The analysis uses the true optimum value and true values of β and σ instead of estimating them, so that it is idealized, but it does show the disappearance of the effect of migration.

8.11 Future directions

There are many limitations of the present framework, and these represent opportunities for further development. Among them are

- This analysis does not take into account the sampling variance of the population means, as it assumes in effect that we observe the population means directly. This can be remedied, as it has been in between-species comparative methods (e.g. in the **Contrast** program in PHYLIP 3.6).
- It is one-character. We can presumably carry things through in a very similar way with vectors of characters instead of scalars. However additive genetic covariances would

then need to be explicitly taken into account. In the current scheme the additive genetic variance is present, but it is assumed constant and hidden in the quantity σ .

- If sampling variance were taken into account, as in point 1, the within-population covariances would be estimated. The shape of the optimum curve would have an effect on the expected within-population covariances, and so will admixture effects due to migration. The quantity σ would be replaced by a matrix, which would depend on additive genetic covariances as well as the shape of the optima.
- Having only one character, we have ignored covariances of characters due to mutation. Mutation will affect the within-population covariances that are used to predict the effect of drift.
- We should think about integrating these inferences with quantitative genetic experiments, so that errors of estimation of the additive genetic covariances and phenotypic covariances can be considered.
- Is there any hope of combining between- and within-species inferences? Can we do comparative methods simultaneously within and between species, using both phylogenies *and* migration matrices? It is hard to imagine what the model would be. If migration matrices differ between species, what should we assume about the migration matrix in the common ancestor of the two species?

All of these challenges need to be addressed; doing so seems worthwhile.

8.12 Conclusion

With molecular sequences and coalescent-based likelihood methods making available good estimates of migration between populations, these can be used to remove artifactual correlations between phenotypes and environmental variables, giving us independent variates when individual population means would be correlated. In effect, we can discover whether neighboring populations are similar because of gene flow or by having similar environments. There are many directions in which the work needs to be expanded, but a start can be made. It is notable that the presence of recombination between loci prevents phylogenetic analysis of sequences from individual loci from serving as the basis for the corrections. In these analyses, migration matrices replace phylogenies as the essential structures.

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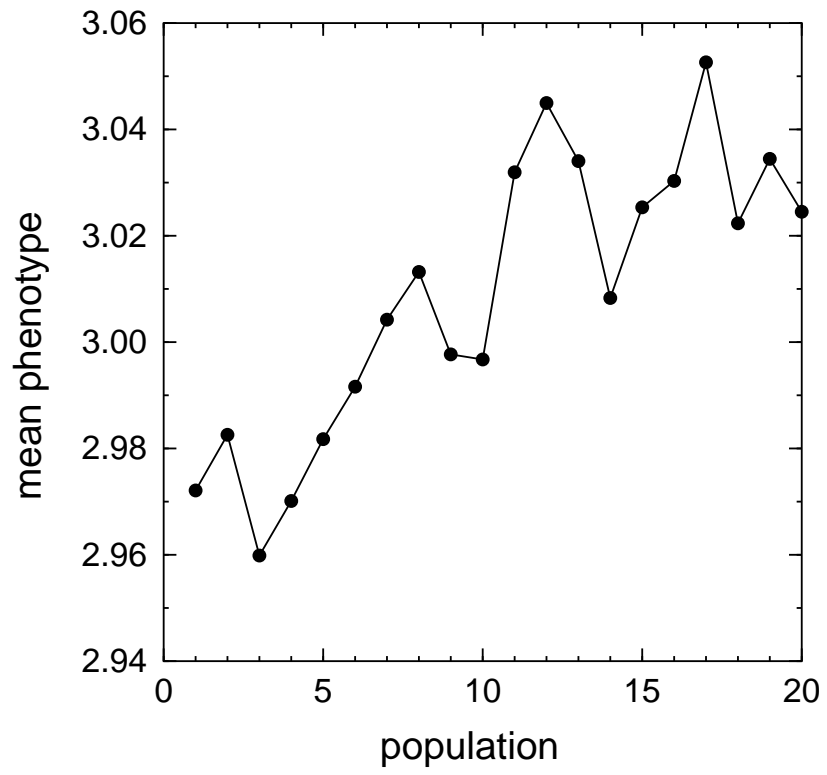
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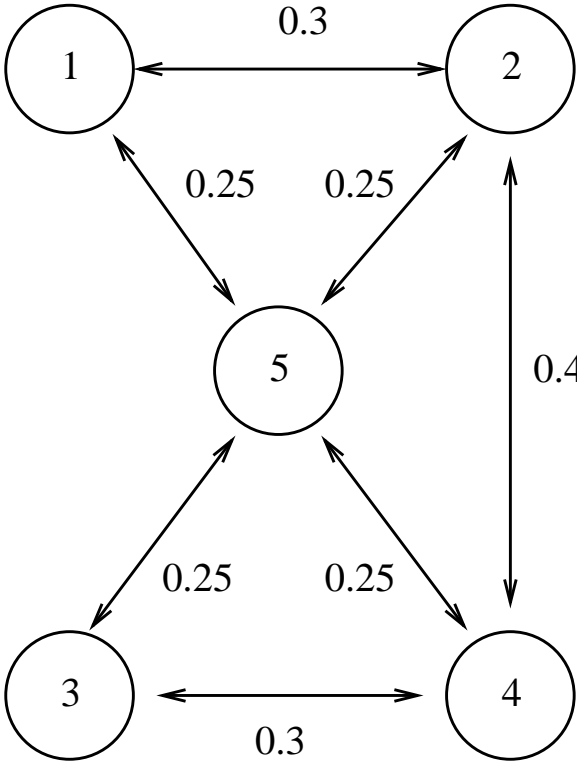
Figure 1. An example data set simulated with a stepping stone model with migration rates 0.01 between adjacent populations, effective population size of all populations 100, $\sigma = 0.01$, and all phenotypic optima equal to 3.

Figure 2. A 5-population pattern of migration whose spectrum is given in the text. The populations are of equal size and the rates of migration are symmetric in this simple case.

Figure 3. 4 of the 5 new coordinates obtained by spectral analysis of the migration matrix in the example. The numerical values of the coefficients are indicated by shading; the actual numerical values are given in the text.

Figure 4. The same data as Figure 1, with the contrast scores computed, each normalized using its expectation and standard deviation. The contrast scores appear to be independently normally distributed with mean 0 and variance 1, as expected.







1.0 0.6 0.2 0 -0.2 -0.6 -1.0

