

Appendix A from R. Holzman et al., “Functional Complexity Can Mitigate Performance Trade-Offs”

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A General Framework to Identify Functional Constraints on the Evolution of Performance

We build on a model of functional constraints on performance evolution (Ghalambor et al. 2004; Walker 2007) to evaluate the consequences of trait covariance and physiological trade-offs for the evolution of performance. Following Ghalambor et al. (2003), we can model performance as a function of multiple independent underlying traits, each one with a given effect on overall performance. Each morphological trait has an independent effect on each performance trait that can be parameterized, for example, using multiple regression models with trait values as the independent variables and performance traits as the dependent variables.

In this context, it can be computationally efficient to use matrix algebra to capture the main effects and constraints of the underlying traits on performance, specifically when a large number of performance and morphological traits are considered. Under this framework, we use the product of two matrixes to determine the overall performance of the system. The first matrix is the \mathbf{F} matrix, which captures the functional architecture of the system by including the effect of each underlying trait on each performance trait (the slope estimate from a multiple regression model). The second matrix is the \mathbf{X} matrix, which includes the trait values for each species in a clade (or individuals in a population). From this matrix, it is straightforward to derive the covariance between traits. Put formally (Ghalambor et al. 2003), n observations (phylogenetic contrasts for $n + 1$ species) for p performance traits can be described by an $n \times p$ performance matrix \mathbf{Q} , in which element q_{ij} is the i th observation for performance trait j . The performance matrix \mathbf{Q} can be modeled as a simple linear function of \mathbf{X} , the $n \times m$ matrix of n observations for m phenotypic (morphological, physiological, or functional) trait values, such that

$$\mathbf{Q} = \mathbf{X}\mathbf{F}. \quad (\text{A1})$$

The matrix \mathbf{F} is the $m \times p$ matrix of performance gradients, which describes the relative effect of each of the m traits in \mathbf{X} on each of the p performance traits in \mathbf{Q} as given, for example, by the partial regression coefficient, b_{jk} , of performance metric j on phenotypic trait k . Trade-offs among performance traits \mathbf{P} can be described by the matrix $\mathbf{P} = \mathbf{Q}^T\mathbf{Q}$, and it follows that

$$\mathbf{P} = (\mathbf{X}\mathbf{F})^T\mathbf{X}\mathbf{F} = \mathbf{F}^T\mathbf{C}\mathbf{F}. \quad (\text{A2})$$

The matrix \mathbf{C} contains the phenotypic trait variances and covariances observed among species given by an $\mathbf{X}^T\mathbf{X}$ matrix multiplication. The matrix \mathbf{P} describes the functional variances and covariances of performance variables that result from the combined effects of the underlying phenotypic traits (Walker 2007). The functional covariances, the off-diagonal elements of \mathbf{P} , represent the functional relationships between pairs of performance variables summed over all phenotypic traits and can be interpreted as net functional trade-offs, if covariance is negative, or facilitations, if it is positive (Ghalambor et al. 2003; Walker 2007). Thus, evolutionary trade-offs (described in \mathbf{P}) are a function of the variances and covariances among phenotypic traits (\mathbf{C}) and the net functional relationships between performance variables ($\mathbf{F}^T\mathbf{F}$).

When simulating a dynamic correlation structure between the performance-determining traits, we repopulated the entire \mathbf{C} matrix each time we increased complexity (i.e., added a trait). To ensure realistic covariance structure between traits, we evaluated the \mathbf{C} matrix according to the following procedure. We generated a pseudo-data matrix in which each column corresponds to a performance-determining trait and each of the 100 rows corresponds to a simulated observed state for that trait (i.e., observations for “species”); a performance trait determined by 10 underlying traits would be represented by a pseudo-data matrix with dimensions 100×10 . Within this matrix, the first trait was a vector, \mathbf{X}_1 , of 100 values drawn from a random normal distribution. Each

additional trait was a vector, \mathbf{X}_n (for $n = 2, 3, \dots, 10$), also composed of 100 observations. To generate correlations between traits, values for each additional trait were modeled as $\mathbf{X}_n = \mathbf{X}_1 \times b_n + \varepsilon \times c_n$. The slope of the relationship between each pair of traits, b_n (the regression slope), was randomly sampled from a continuous uniform distribution $(-1, 1)$ separately for each new trait. The strength of the correlation between traits (R^2) was allowed to vary and was determined by the residuals of the regression, $\varepsilon \times c_n$, where the vector ε was drawn from a random normal distribution, and c_n is a scaling parameter drawn from continuous uniform distribution $(0, 1)$ once per each new trait. The resulting \mathbf{C} matrix, $n \times n$ for n performance-determining traits, was calculated as the covariance matrix for a $100 \times n$ pseudo-data matrix, such that the covariance $c_{i,j}$ between traits i and j is the cross-covariance between the trait vectors \mathbf{X}_i and \mathbf{X}_j .