

The adaptive change in the
“ecological characteristics” \mathbf{e}_i

$$\frac{d\mathbf{e}_i}{dt} = \gamma \hat{X}_i \bar{\mathbf{S}}(\mathbf{e}_i)$$

is not in the “ideal” direction

$$\mathbf{S}(\mathbf{e}_i)$$

but in the ideal direction
constrained by the available
variation in \mathbf{p}_i :

$$\bar{\mathbf{S}}(\mathbf{e}_i) = \frac{\partial \mathbf{e}_i}{\partial \mathbf{p}_i} \frac{\partial \mathbf{e}_i}{\partial \mathbf{p}_i}^T \mathbf{S}(\mathbf{e}_i)$$