

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  $\mathbf{p}_i$ :

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