Evolution of Spatial Correlations among Interacting Species

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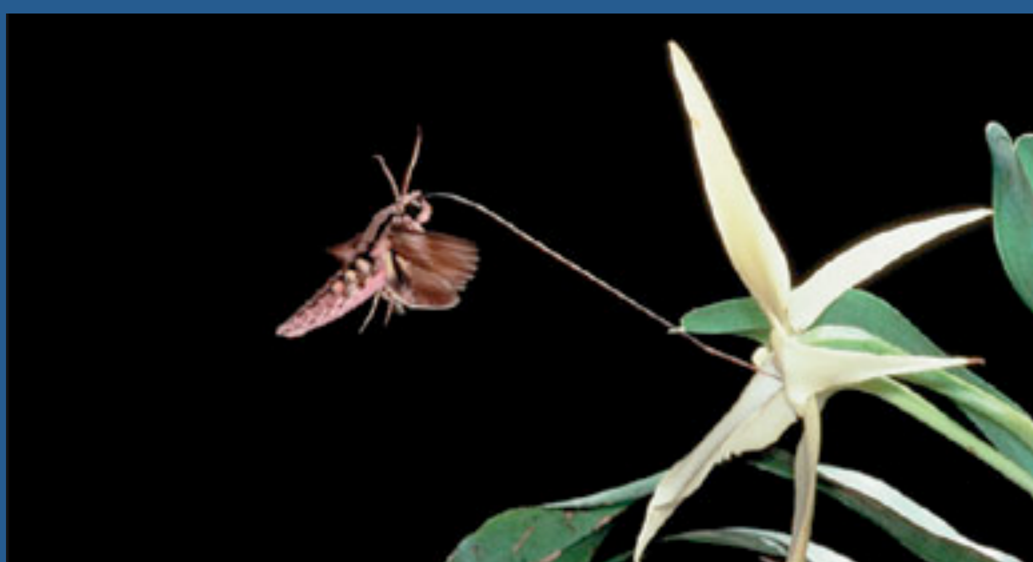
Coevolution

Joint adaptive evolution of species in response to reciprocal interspecific selection

(Janzen 1980)



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Coevolution & Correlation

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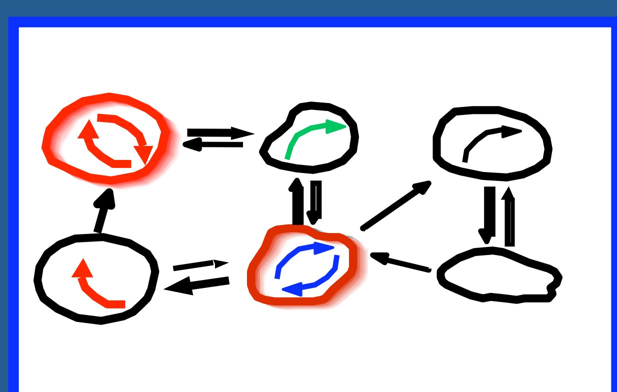
- Coevolution can cause strong correlations between traits of different species
- Coevolution often assumed the cause of strong inter-specific correlations
- Janzen 1980: Correlation need not imply coevolution

Objectives & Questions

- Quantitatively justify Janzen's verbal arguments
- Use results to address:
  1. When will correlation imply coevolution?
  2. Does absence of correlation imply absence of coevolution?
  3. Are correlations useful for evaluating the Geographic Mosaic Theory?

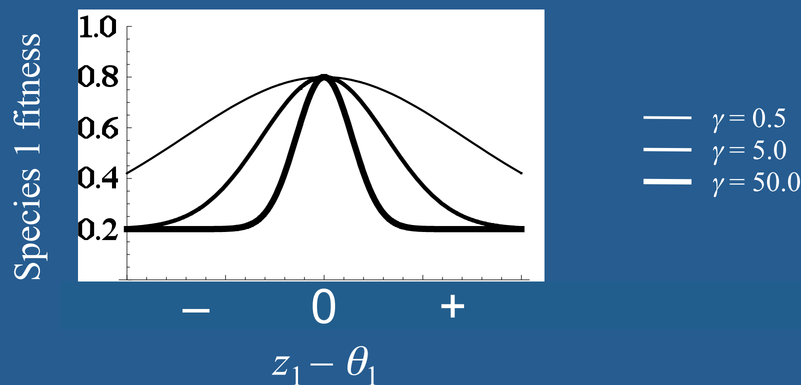


Modeling Approach

- Two species
  - Co-distributed in finite populations across large, discrete set of variable sites
- Local abiotic & biotic selection
  - depend on quantitative traits, z_1 & z_2
  - spatially co-variable abiotic selection
- Random genetic drift
- Gene flow among sites

Abiotic selection

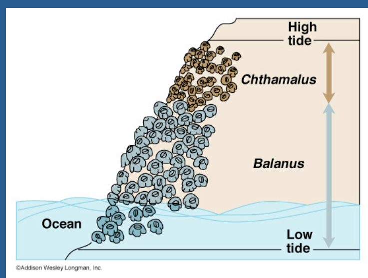
$$W_{\text{abiotic},i}(z_i) \propto \exp\left[-\gamma_i (z_i - \theta_i)^2\right]$$



$$\begin{pmatrix}\theta_1\\ \theta_2\end{pmatrix} \sim \text{Normal}\left[\begin{pmatrix}\theta_1\\ \theta_2\end{pmatrix}; \begin{pmatrix}\sigma_{\theta_1}^2 & \sigma_{\theta_1\theta_2}\\ \sigma_{\theta_1\theta_2} & \sigma_{\theta_2}^2\end{pmatrix}\right]$$

Optima spatially variable, temporally fixed

Biotic Selection



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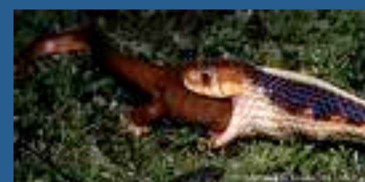
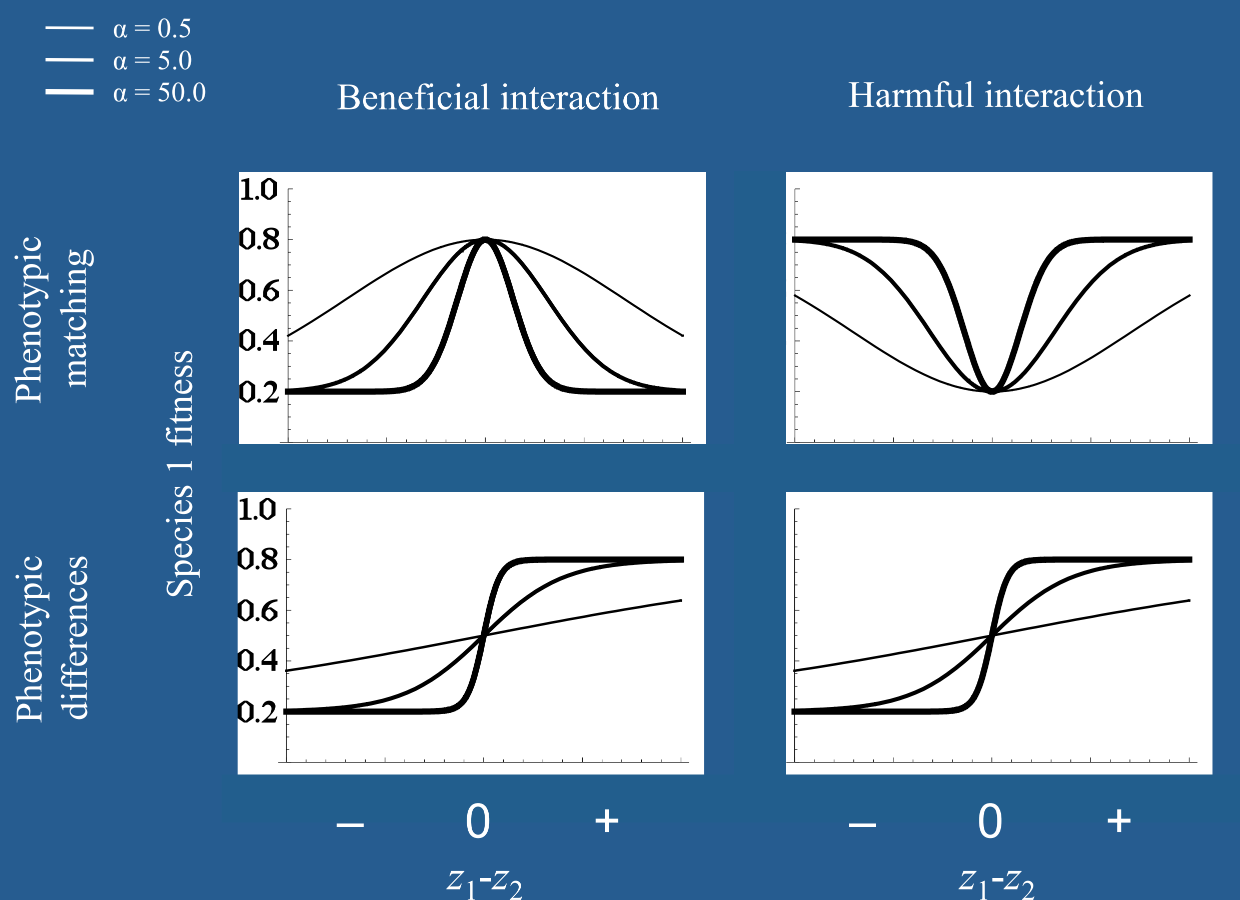
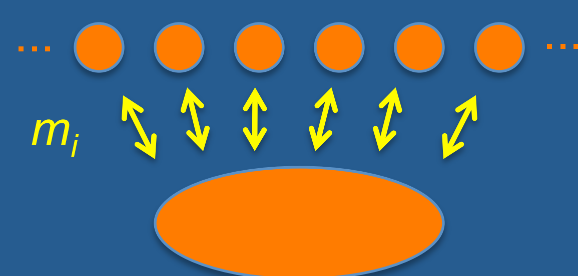




Drift & Gene Flow

- Random Genetic Drift
  - Fixed local sizes n_1 & n_2
  - Local change in $\bar{z}_i$ due to drift:
    - $E(\Delta\bar{z}_i) = 0$
    - $V(\Delta\bar{z}_i) = G_i/n_i$
      - G_i additive-genetic variance for z_i



- Gene flow
  - Wright's island model
  - rates m_1 & m_2

Approximate Analysis

- Assumptions:
  - fitness weakly sensitive to phenotype differences [α, $\gamma = O(\varepsilon)$, $\varepsilon << 1$]
  - fitness functions well-approximated by 1st-order Taylor series in ε
  - additive-genetic variances (G_i) fixed
  - traits normally distributed
  - weak gene flow [$m_i = O(\varepsilon)$]
  - abiotic optima vary weakly [$\sigma^2_{\vartheta} = O(\varepsilon)$]
- Aggregate variables followed:
  - Grand trait means, variances
  - Covariances among…
    - local trait mean & abiotic optima
    - local trait means of both species

Phenotype Matching Model: Local Dynamics

$$\Delta\bar{z}_{i,t+1} \approx m\left(\mu_{i,t} - \bar{z}_{i,t}\right) + G_i \frac{\partial \ln \overline{W}_i}{d\bar{z}_{i,t}} + \zeta_i$$

gene flow selection drift

$$\mu_{i,t} = \mathrm{E}\left(\bar{z}_{i,t}\right)$$

$$W_i(z_i | z_j) = \exp[-\gamma_i (z_i - \theta_i)^2]\left\{K_i + \xi_i \exp[-\alpha(z_i - z_j)^2])\right\}$$

abiotic biotic

$$\overline{W}_i = \int\int W_i\left(z_i | z_j\right)\phi_i(z_i)\phi_j\left(z_j\right) dz_i dz_j$$

$$\mathrm{E}\left(\zeta_i\right) = 0,\ \ \mathrm{var}\left(\zeta_i\right) = G_i / n_i$$

Phenotype Matching Model: Aggregate Dynamics

$$\Delta\mu_{i,t} = \mathrm{E}\left(\Delta\bar{z}_{i,t}\right) \approx 2G_i\left[\gamma_i\left(\bar{\theta}_i - \mu_i\right) + s_i\left(\mu_{j,t} - \mu_{i,t}\right)\right]$$

$$s_i = \alpha_i\xi_i/\left(K_i + \xi_i\right)$$

$$\begin{aligned}\Delta\sigma^2_{\bar{z}_i} &= \mathrm{var}\left(\bar{z}_i + \Delta\bar{z}_i\right) - \sigma^2_{\bar{z}_i} \\ &\approx 4G_i\left(1 - m_i\right)\left\{\gamma_i\left[\sigma_{\bar{z}_i\theta_i} - \left(1 - m_i\right)\sigma^2_{\bar{z}_i}\right] + s_i\left[\left(1 - m_j\right)\sigma_{\bar{z}_1\bar{z}_2} - \left(1 - m_i\right)\sigma^2_{\bar{z}_i}\right]\right\} \\ &\quad - \left(2m_i - m_i^2\right)\sigma^2_{\bar{z}_i} + G_i/n_i\end{aligned}$$

$$\begin{aligned}\Delta\sigma_{\bar{z}_i\theta_i} &= \mathrm{cov}\left(\Delta\bar{z}_i, \theta_i\right) \\ &\approx 2G_i\left\{\gamma_i\left[\sigma^2_{\theta_i} - \left(1 - m_i\right)\sigma_{\bar{z}_i\theta_i}\right] + s_i\left[\left(1 - m_j\right)\sigma_{\bar{z}_j\theta_i} - \left(1 - m_i\right)\sigma_{\bar{z}_i\theta_i}\right]\right\} - m_i\sigma_{\bar{z}_i\theta_i}\end{aligned}$$

$$\begin{aligned}\Delta\sigma_{\bar{z}_i\theta_j} &= \mathrm{cov}\left(\Delta\bar{z}_i, \theta_j\right) \\ &\approx 2G_i\left\{\gamma_j\left[\sigma_{\theta_1\theta_2} - \left(1 - m_i\right)\sigma_{\bar{z}_i\theta_j}\right] + s_i\left[\left(1 - m_j\right)\sigma_{\bar{z}_j\theta_j} - \left(1 - m_i\right)\sigma_{\bar{z}_i\theta_j}\right]\right\} - m_i\sigma_{\bar{z}_i\theta_j}\end{aligned}$$

$$\begin{aligned}\Delta\sigma_{\bar{z}_1\bar{z}_2} &= \mathrm{cov}\left(\bar{z}_1 + \Delta\bar{z}_1, \bar{z}_2 + \Delta\bar{z}_2\right) - \sigma_{\bar{z}_1\bar{z}_2} \\ &\approx 2G_1\left(1 - m_2\right)\left\{\gamma_1\left[\sigma_{\bar{z}_2\theta_1} - \left(1 - m_1\right)\sigma_{\bar{z}_1\bar{z}_2}\right] + s_1\left[\left(1 - m_2\right)\sigma^2_{\bar{z}_2} - \left(1 - m_1\right)\sigma_{\bar{z}_1\bar{z}_2}\right]\right\} \\ &\quad + 2G_2\left(1 - m_1\right)\left\{\gamma_2\left[\sigma_{\bar{z}_1\theta_2} - \left(1 - m_2\right)\sigma_{\bar{z}_1\bar{z}_2}\right] + s_2\left[\left(1 - m_1\right)\sigma^2_{\bar{z}_1} - \left(1 - m_2\right)\sigma_{\bar{z}_1\bar{z}_2}\right]\right\} \\ &\quad - \left(m_1 + m_2 - m_1m_2\right)\sigma_{\bar{z}_1\bar{z}_2}\end{aligned}$$

Analytic Results

- Phenotype differences
  - Moments always equilibrate
  - Equilibrium interspecific covariance:

$$\hat{\sigma}_{\bar{z}_1\bar{z}_2} = 0 + O(\varepsilon^2)$$

- Phenotype Matching
  - Moments equilibrate or evolve without bound
  - Equilibrium interspecific covariance:

$$\hat{\sigma}_{\bar{z}_1\bar{z}_2} = \frac{2\left(G_1 s_{M1}\hat{\sigma}^2_{\bar{z}_2} + G_2 s_{M2}\hat{\sigma}^2_{\bar{z}_1}\right)}{m_1 + m_2 + 2\left(G_1\left(s_{M1} + \gamma_1\right) + G_2\left(s_{M2} + \gamma_2\right)\right)} + O(\varepsilon^2)$$

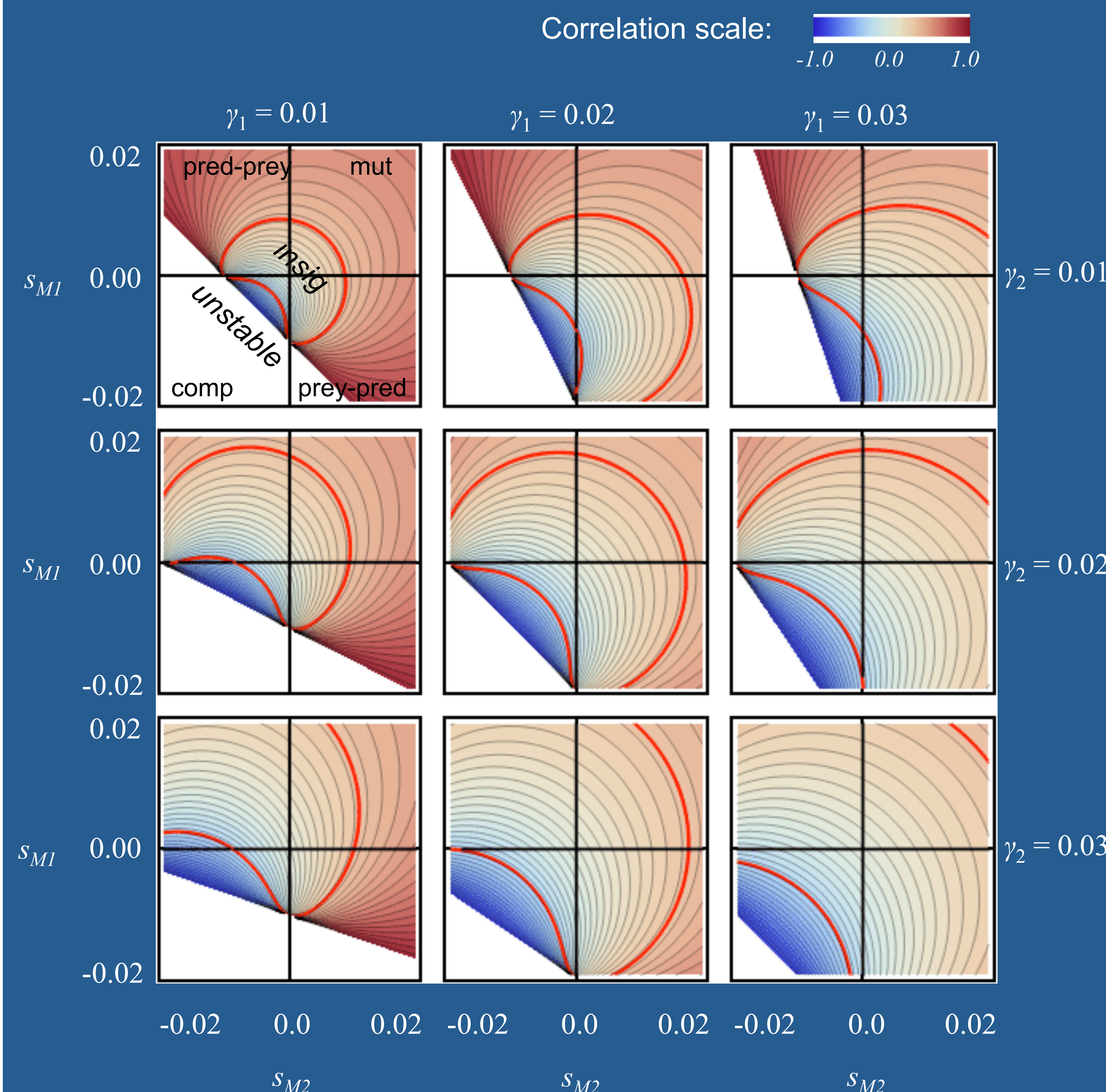
Individual-Based Simulations

- Track movement, reproduction,biotic & abiotic selection of individual phenotypes

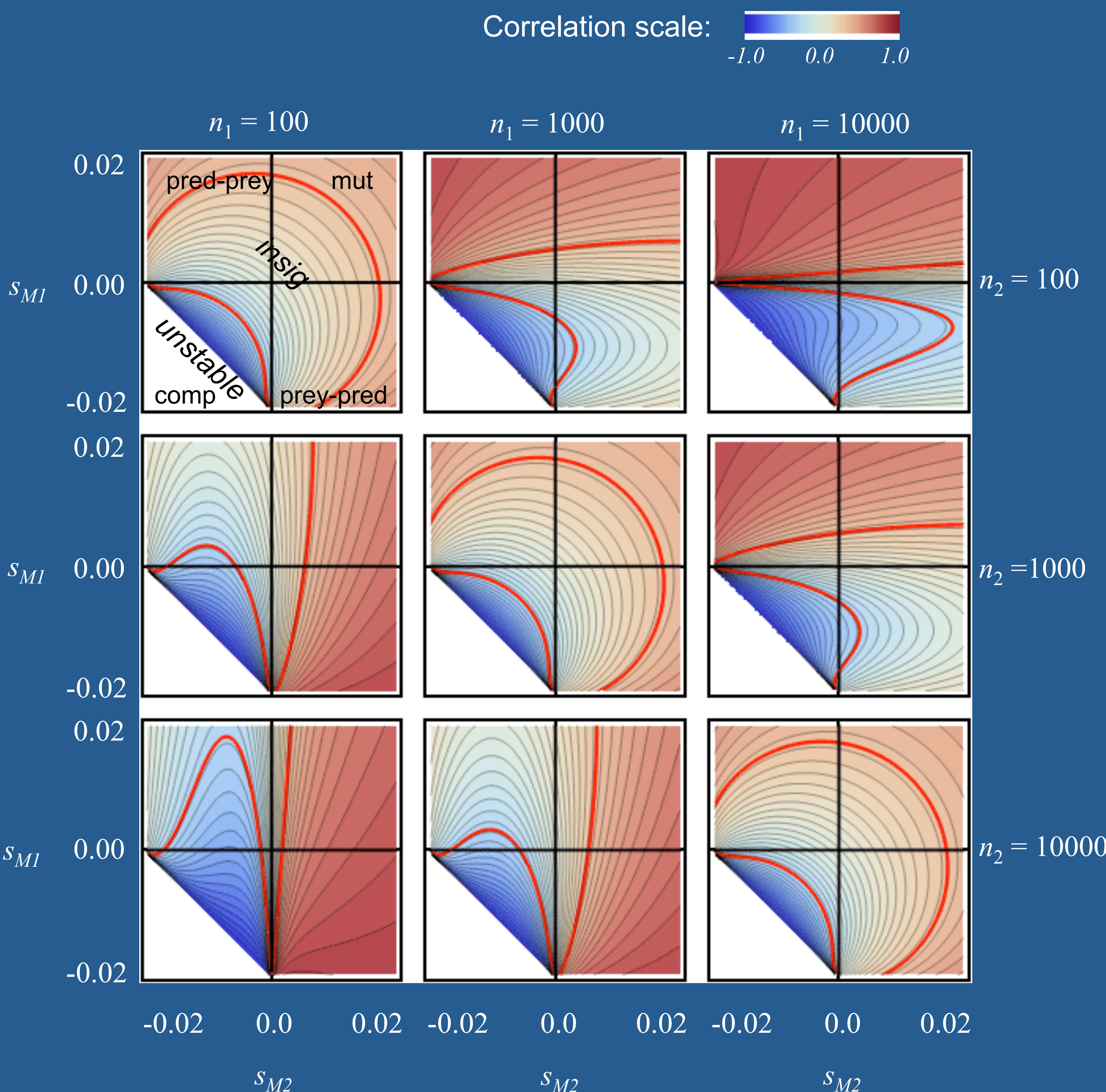
- Infinitesimal model of inheritance
  - Accommodates arbitrary phenotype distributions & speeds computation

- IBM approach allows:
  - Strong evolutionary forces and substantial environmental variability
  - Dynamic additive-genetic variances

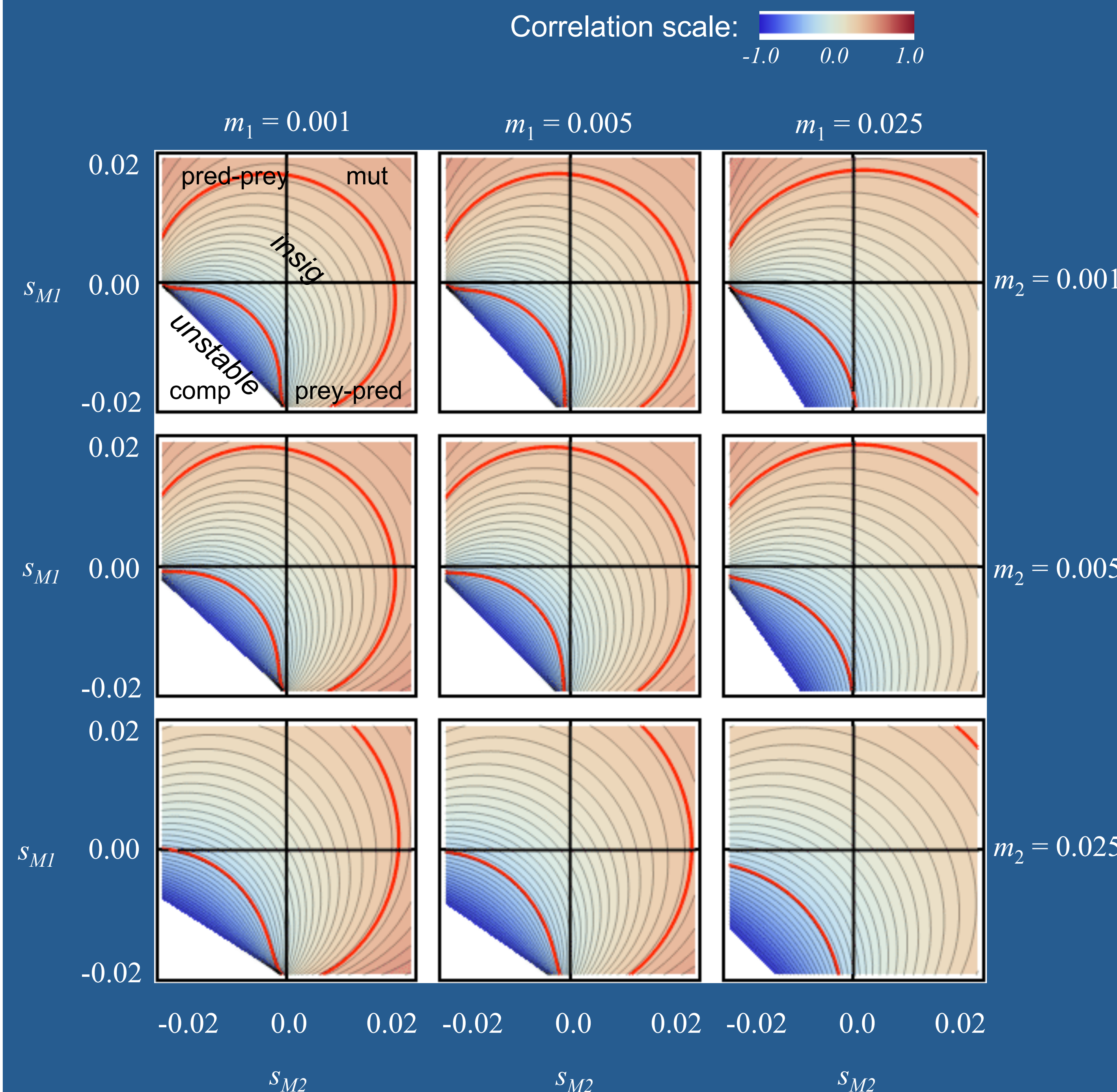
Correlation vs Biotic Selection:
impact of abiotic selection



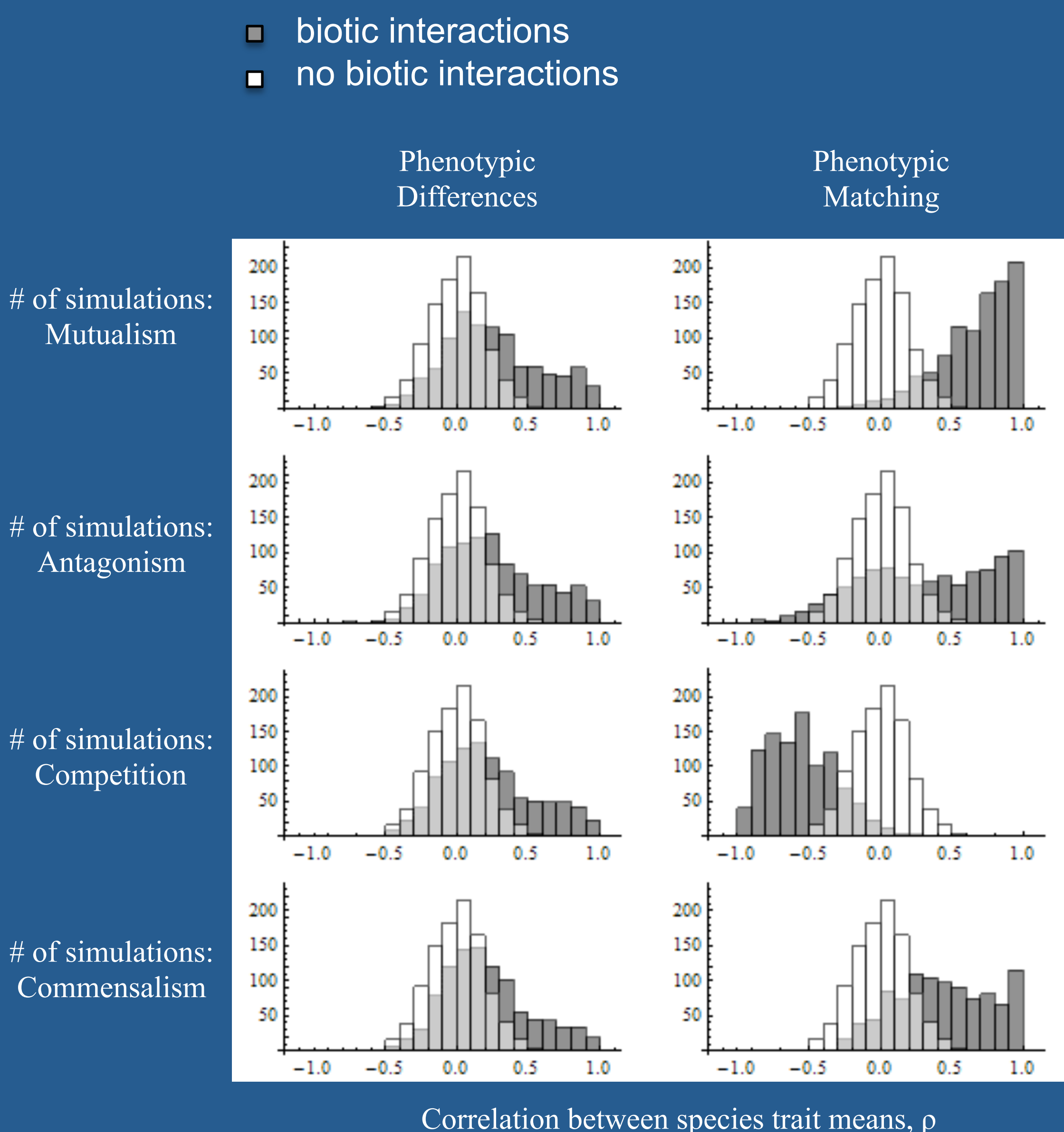
Correlation vs Biotic Selection: *impact of drift*



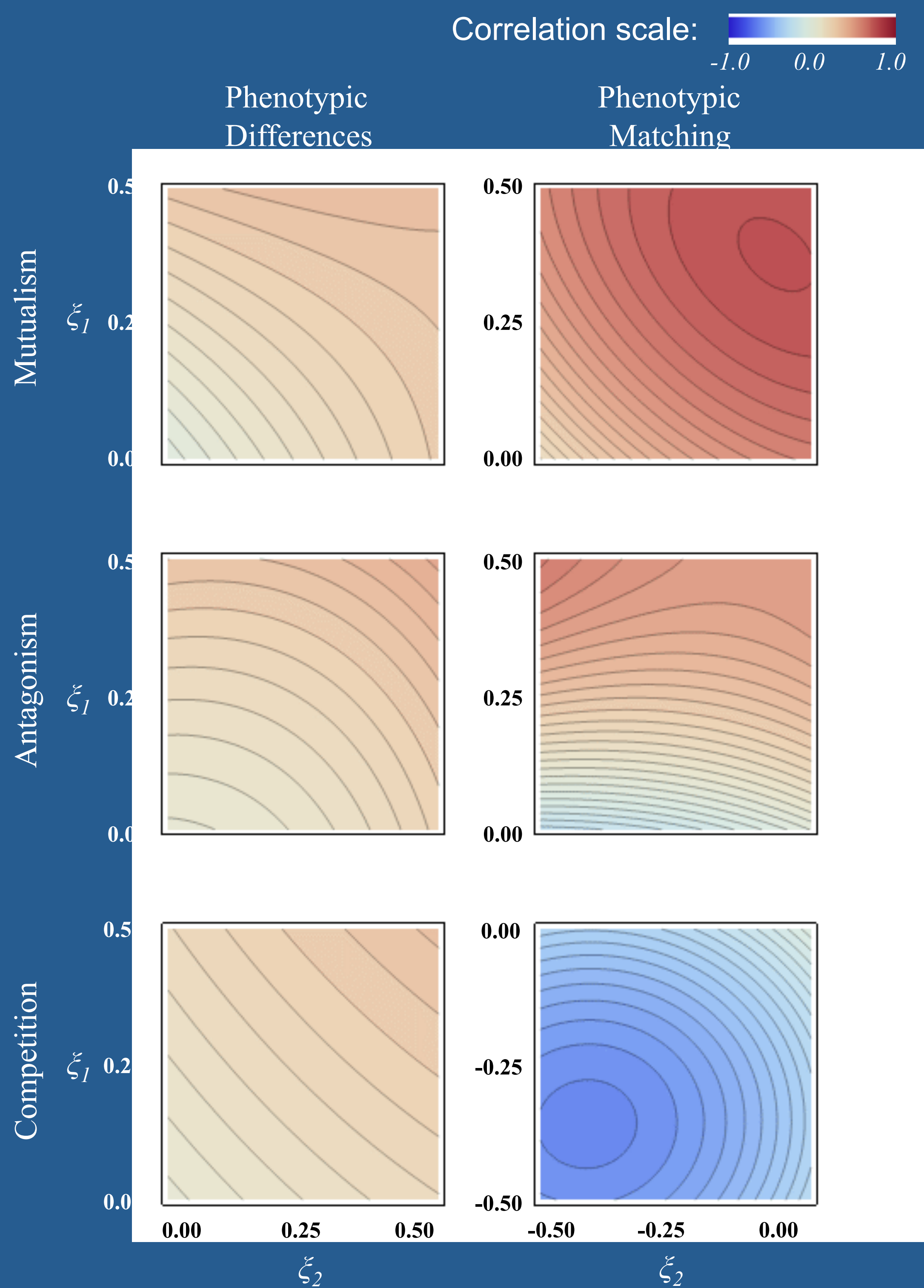
Correlation vs Biotic Selection: *impact of gene flow*



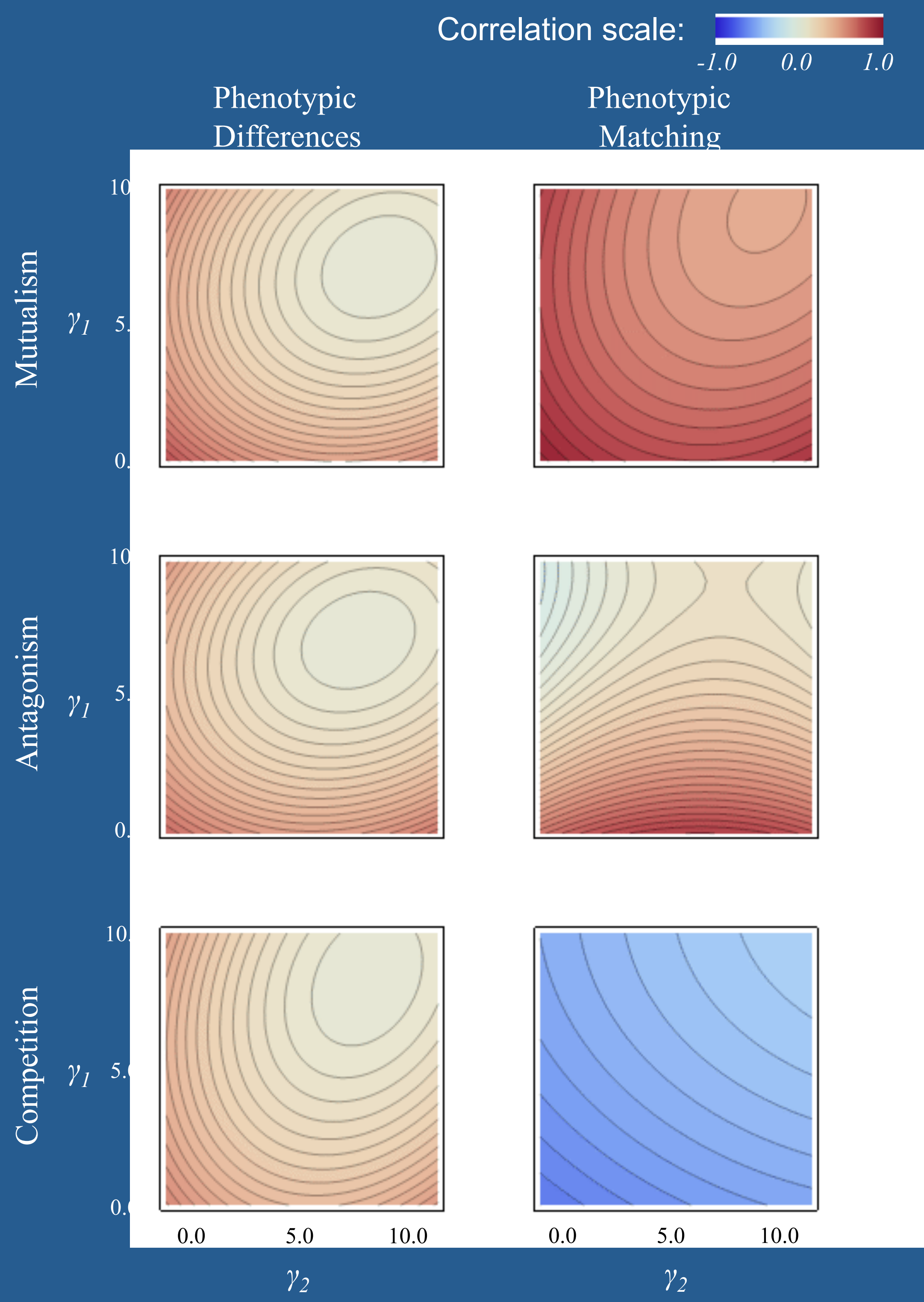
Abiotic vs Biotic Selection



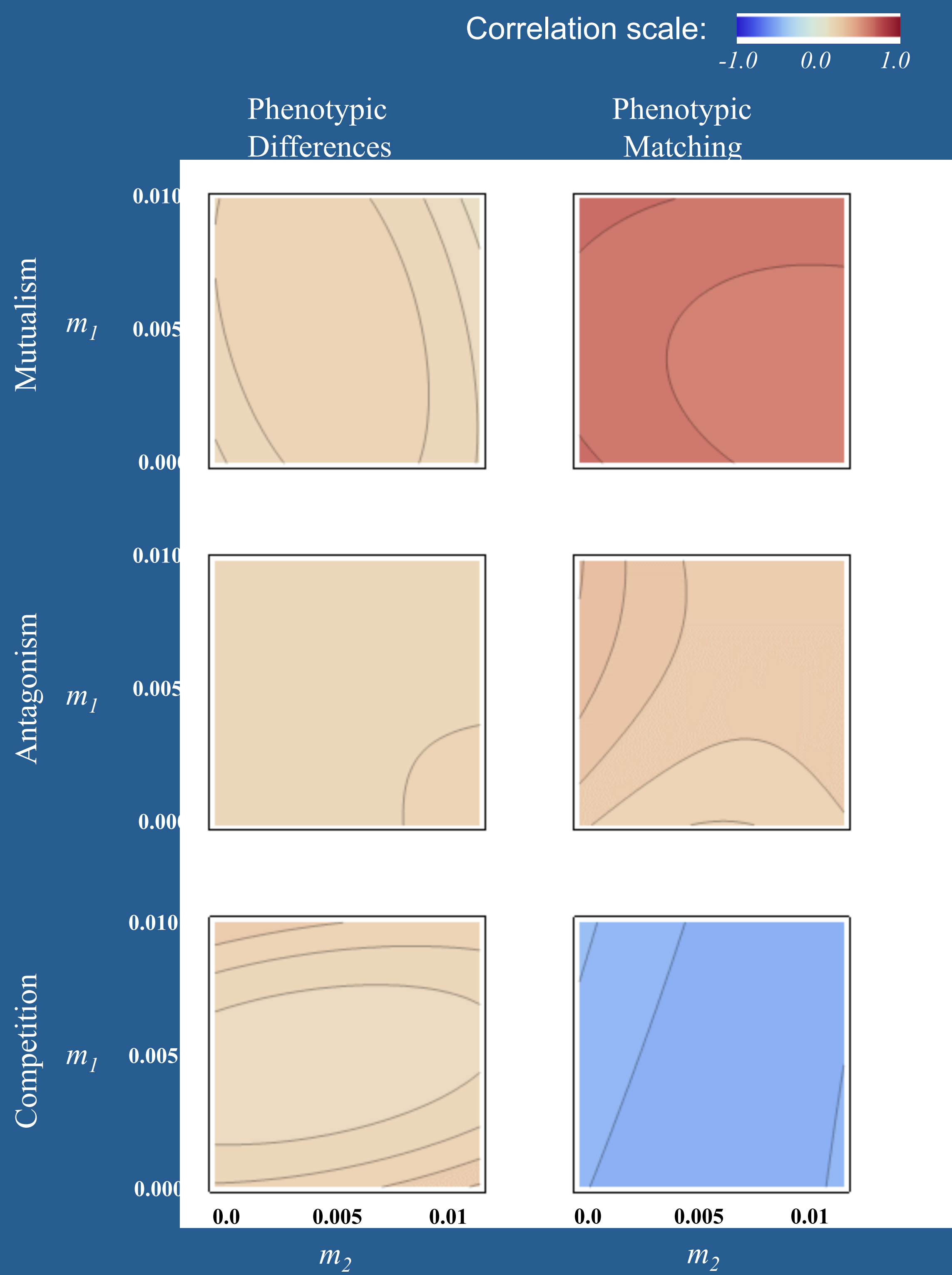
Correlation vs Biotic Selection: *IBM results*



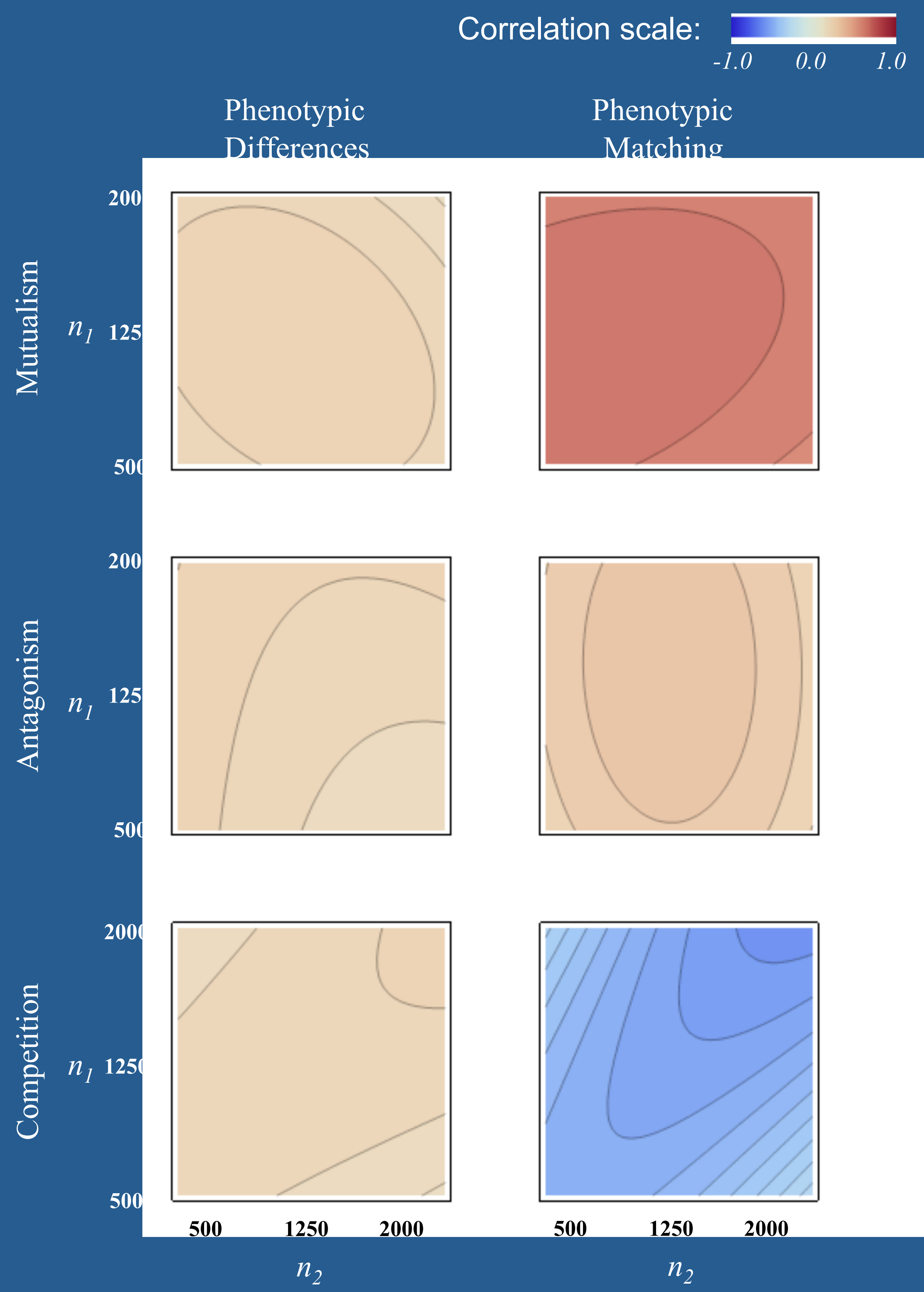
Correlation vs Abiotic Selection:
IBM results



Correlation vs Gene Flow: *IBM results*



Correlation vs Drift:
IBM results



Main Findings

- Detectable correlations require:
  - Biotic selection strong relative to abiotic selection
    - Also absolutely strong for phenotypic diffferences
- Correlation need not imply coevolution (Janzen verified)
- Coevolution need not imply correlation
- Correlations inclusive about Geographic Mosaic Theory

Open Questions

- Findings suggested fixed migration has little impact on interspecific correlations
  - Especially compared with drift
- How might adaptive movement in one or both species alter this conclusion?
  - Joint evolution of gene flow rates and phenotypes
  - Joint evolution of “context dependent” movement
- Impacts of coupled population dynamics?
  - Would influence drift, realized gene flow, patterns of interaction and selection, persistence, etc. [“metacommunity coevolution” perspective]

Acknowledgements

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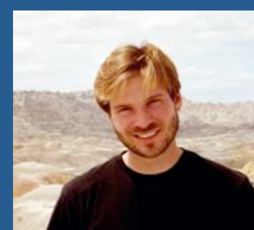

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