Deleterious CAFI Promote More Small and Large Corals in Reefs

An analysis of a spatially well-mixed, deterministic, partial differential equation model of the size-density of coral reefs

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Biological Assumptions

Our Coral Reef

- Space limited
- Corals are uniformly spread in environment, cannot overlap
  - Coral growth dependent on available space
- Corals enter only through immigration, dependent on available space
- Coral associated fish and invertebrates (CAFI) occupy the reef
  - Can be beneficial, neutral, deleterious
  - Influence coral growth rate and life expectancy

Spatially well-mixed deterministic PDE

Model Definition

- $u(r, t)dr$ the number of corals with radius size between $(r, r + dr)$ at time t
- $\gamma(A, r)$ growth, $\mu(A, r)$ mortality, $\Gamma(A)$ immigration
- Initial Boundary Value Problem:

$$\begin{aligned} \partial_t u(r, t) + \partial_r \left(\gamma(A(t), r)u(r, t)\right) &= -\mu(A, r)u(r, t) \\ u(r,0) &= u_0(r) \\ \gamma(A(t),0)u(0,t) &= \Gamma(A(t)) \\ A(t) &= \int_0^{r_m} \pi r^2 u(r, t)dr \end{aligned}$$

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CAFI Assumptions

- CAFI immigrate during settlement events every Δ days
- CAFI settlement rate, $\lambda(r, A)$ depends on coral size and area occupied by size-density
- CAFI leave through density independent, α, density dependent, β, mortality

$$\frac{dX(t; r, A)}{dt} = -\alpha X - \pi r^2 \beta X^2 + \frac{1}{\pi r^2} \sum_{k=0}^{\infty} \lambda(r, A) \delta_{k\Delta}(t)$$

$$X(0; r, A) = X_0$$

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CAFI Computation

- Fix r, A, then $X(t; r, A)$ converges to steady state for $t \in [k\Delta, (k+1)\Delta)$
- Define average CAFI density given coral size and area occupied

$$\bar{X}(r, A) = \text{avg}_{t \in [k\Delta, (k+1)\Delta)} \{X(t; r, A)\}$$

- Use Hill Equation for CAFI effect, $\phi \in (-1, 1)$

$$\mathscr{E}(r, A) = 1 + \phi \left(\frac{\bar{X}^{\beta_X}(r, A)}{\theta_X^{\beta_X} + \bar{X}^{\beta_X}(r, A)} \right)$$

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CAFI, Area Dependent Growth and Life Expectancy

- Corals cannot overlap => growth rate slows when space is limited

$$\gamma(A(t), r) = \gamma_0 \left[1 - \left(\frac{A(t)}{A_m} \right)^{n_g} \right] \mathcal{E}(r, A(t))$$

- Small corals have lower life expectancy than large corals

$$L(A(t), r) = \left[L_{\text{min}} + \left(L_{\text{max}} - L_{\text{min}} \right) \left(\frac{r^{\beta_L}}{\theta_L^{\beta_L} + r^{\beta_L}} \right) \right] \mathcal{E}(r, A(t))$$

$$\mu(A(t), r) = 1/L(r, A(t))$$

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Area Dependent Immigration

- Coral larva can only land on available space, finite number of attempts to land
- After the finite attempts the larva expire

$$\Gamma(A(t)) = \Gamma_0 \left[1 - \left(\frac{A(t)}{A_m} \right)^{n_I} \right]$$

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Existence, Uniqueness of Solution

- Previous definitions of growth, mortality, immigration, CAFI effect ensure Lipschitz continuity wrt r, A

- **Theorem:** $u(r, t)$ *has a unique solution for all positive time* t*.*
    - Contraction mapping argument

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Steady State Solution

- Redefine IBVP for stationary solution $\bar{u}(r)$

$$\partial_r \left(\gamma(A, r)\bar{u}(r)\right) = -\mu(r, A)\bar{u}(r)$$

$$\gamma(A,0)\bar{u}(0) = \Gamma(A)$$

$$A = \int_0^{r_m} \pi r^2 \bar{u}(r) dr$$

- Solve through separation of variables, integrating factor

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Conditional Convergence to Steady State Solution

- Assume that $\lim_{t \to \infty} A(t) = A$

- **Theorem:** *If $A(t)$ converges to A, then $u(r, t) \to \bar{u}(r)$ in L1.*

- Showing the existence of a limit point of $A(t)$ is difficult, potential oscillations

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Numerical Solution Method

- Upwind scheme: ($u(r_j, t_n) \approx U_j^n$)

$$U_j^{n+1} = U_j^n - \frac{\Delta t \gamma_j^n}{\Delta r}\left[U_j^n - U_{j-1}^n\right] - \Delta t\left(\mu_j^n + d\gamma_j^n\right)U_j^n$$

- Trapezoidal method for area: ($A(t_n) \approx A_n$)

$$A_n \approx \frac{\pi \Delta r}{2}\left(r_0^2 U_0^n + 2\sum_{j=1}^{J-1} r_j^2 U_j^n + r_J^2 U_J^n\right)$$

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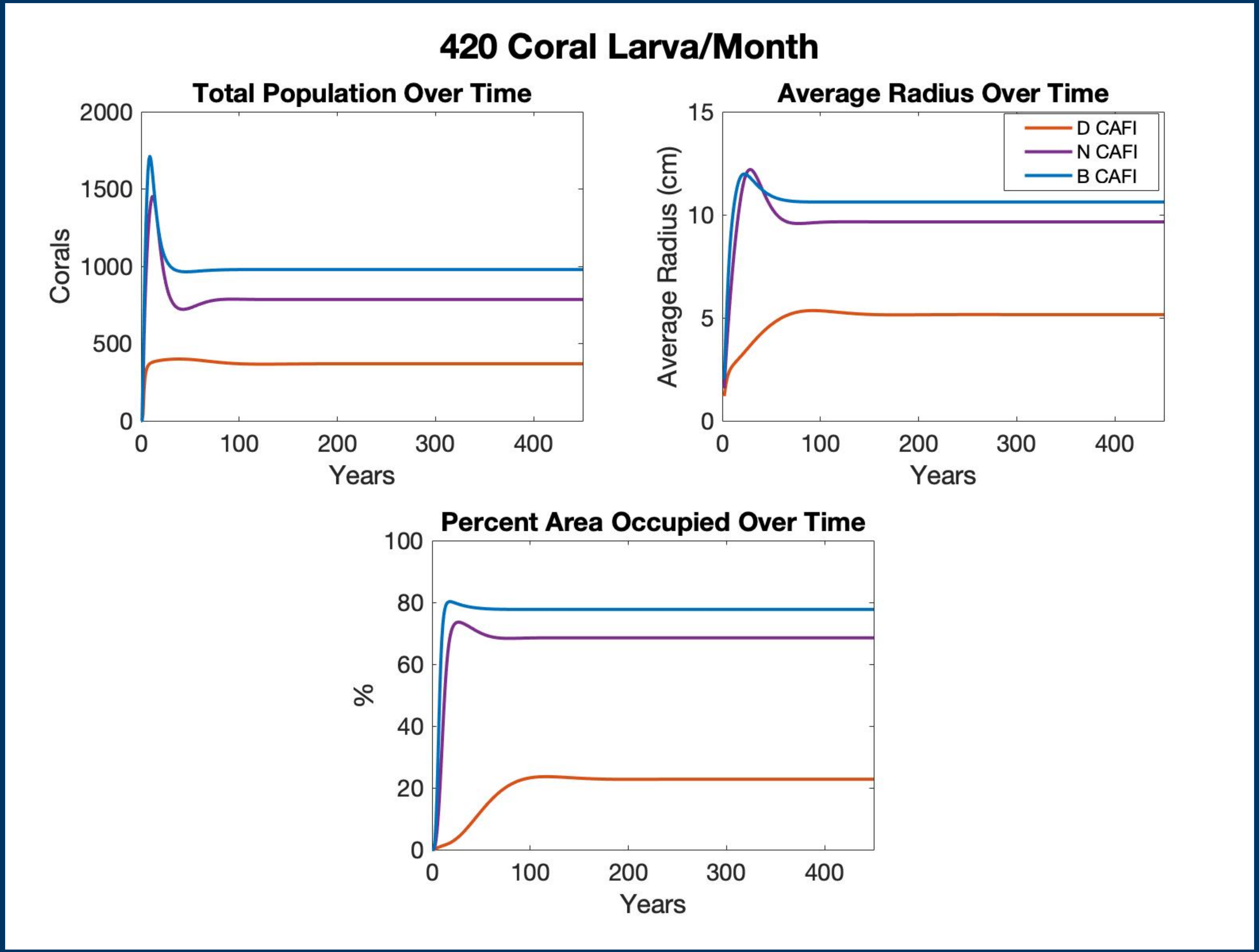
Convergence to Steady State (SI Figure)



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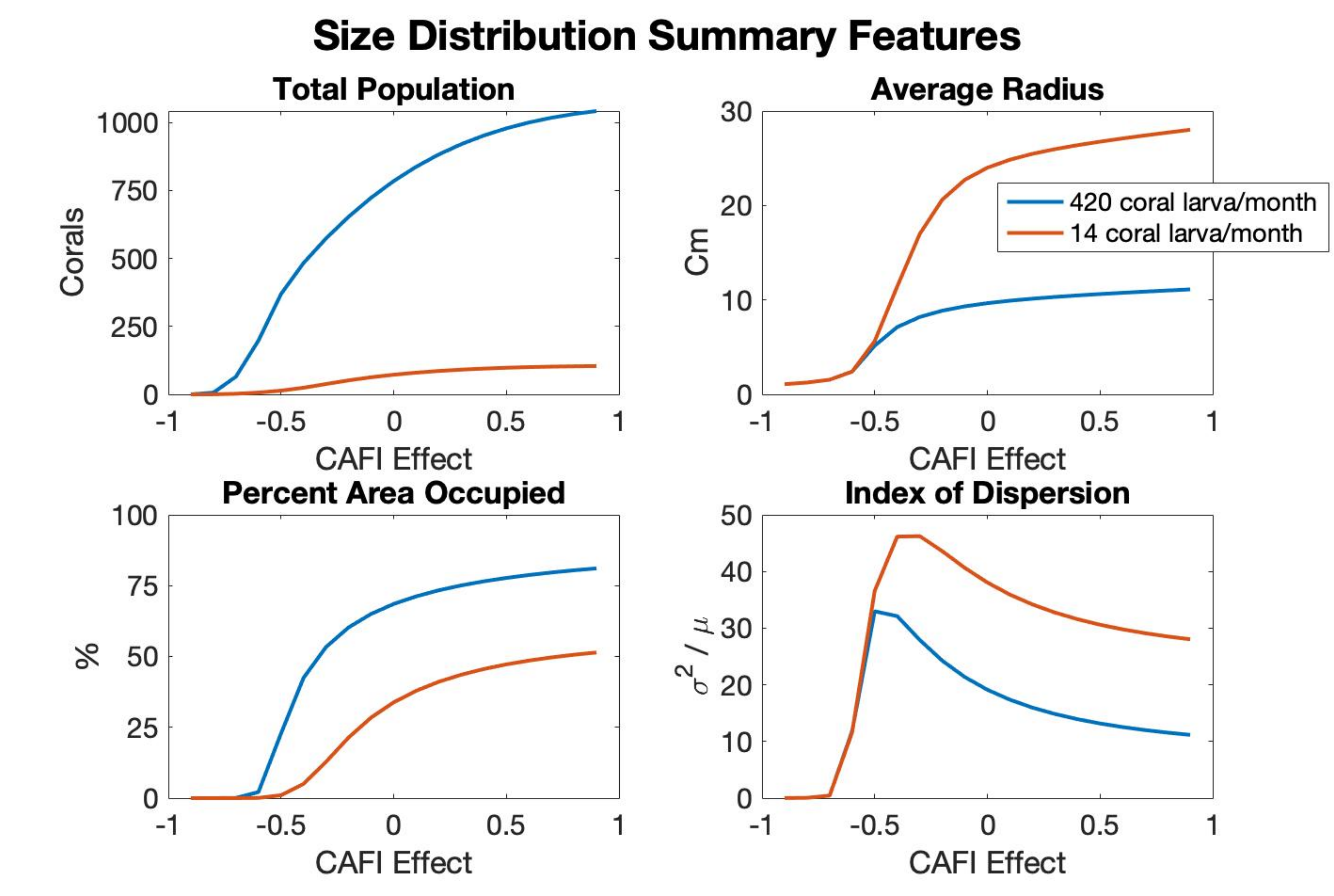
Summary Features of Steady State Solution



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Visualizing the Steady State Solution of the Size-Density

- Assume that total number of corals in an environment is a Poisson RV

$$N \sim \text{Poi}\left(\Delta r \sum_{j=0}^{J} U_j^N\right)$$

- Number of corals with radius size $r \in [j\Delta r, (j+1)\Delta r)$

$$N_j \sim \text{Poi}\left(\Delta r U_j^N\right)$$

- Sort radius samples and uniformly place w/o overlap

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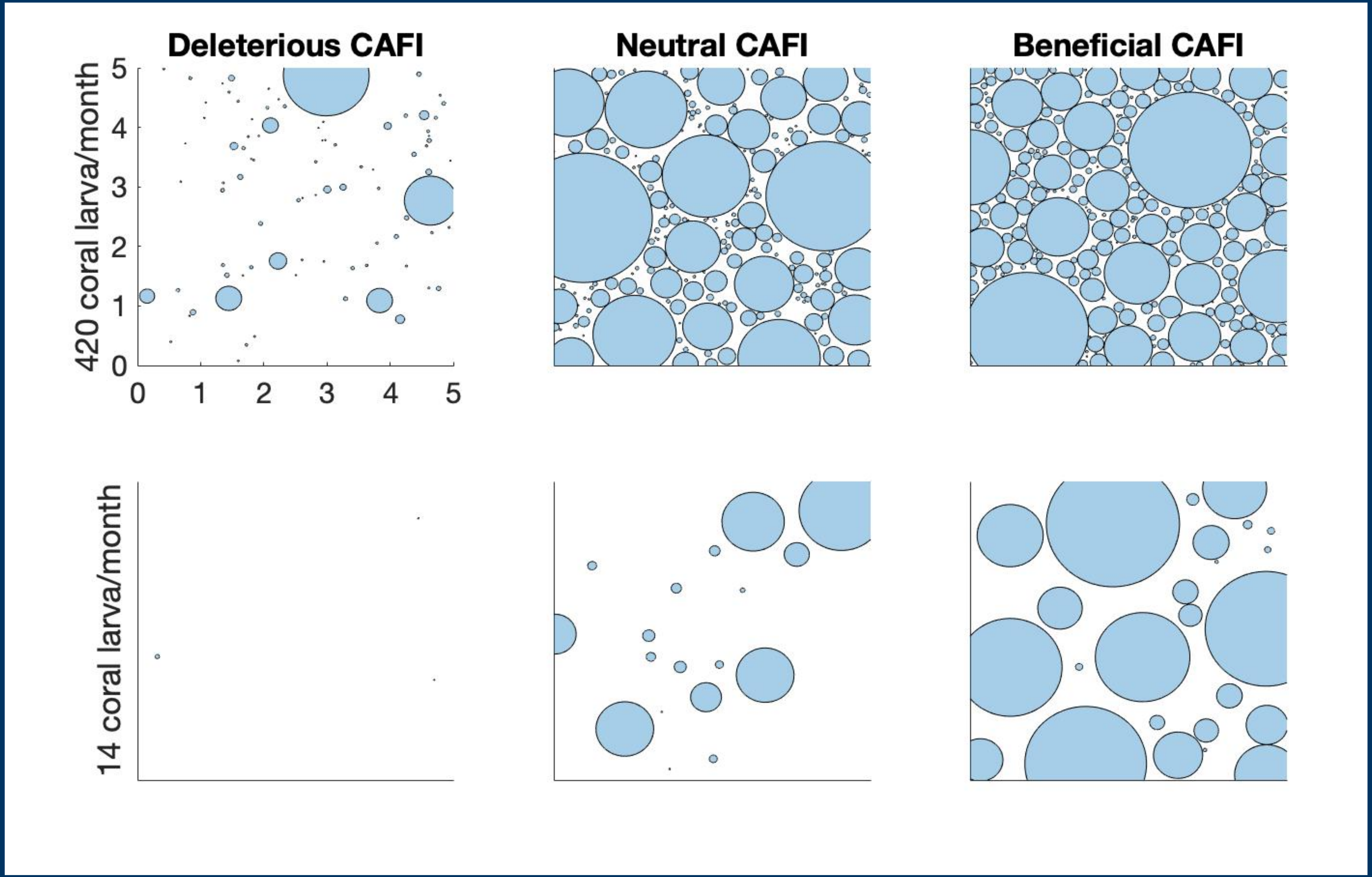
Visualizing the Size-Density-Sample Environments



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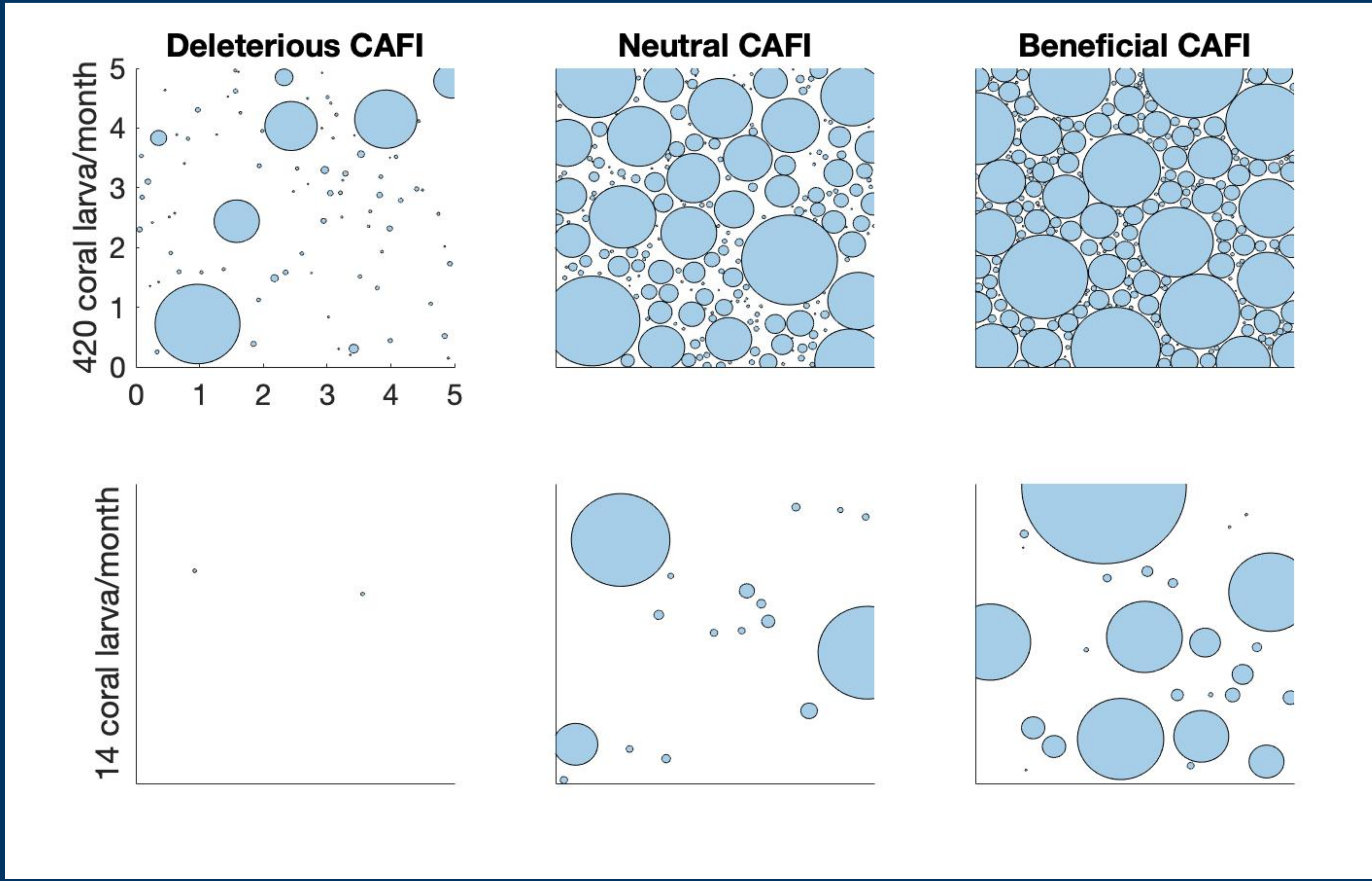
Visualizing the Size-Density-Sample Environments



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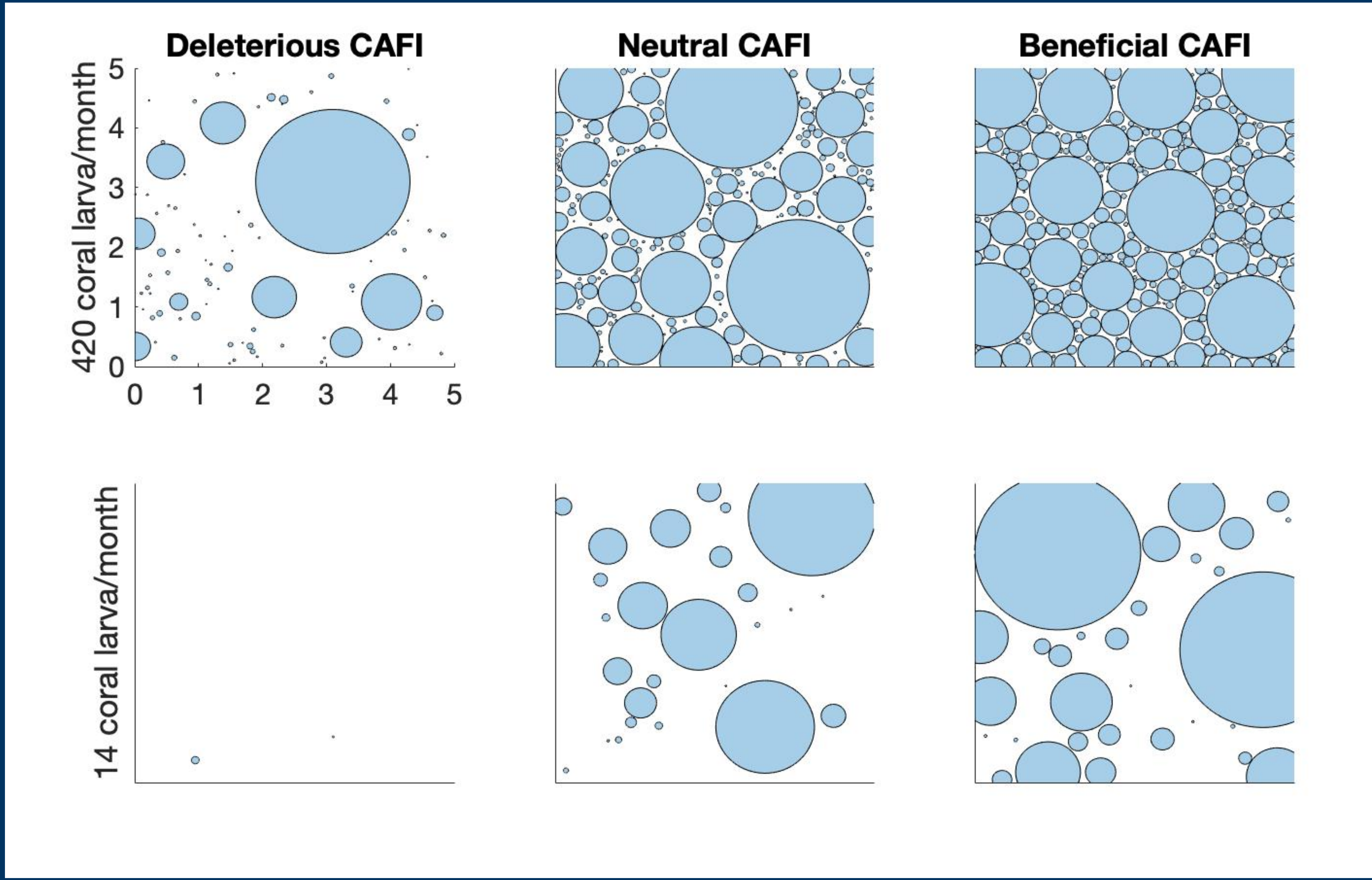
Visualizing the Size-Density-Sample Environments



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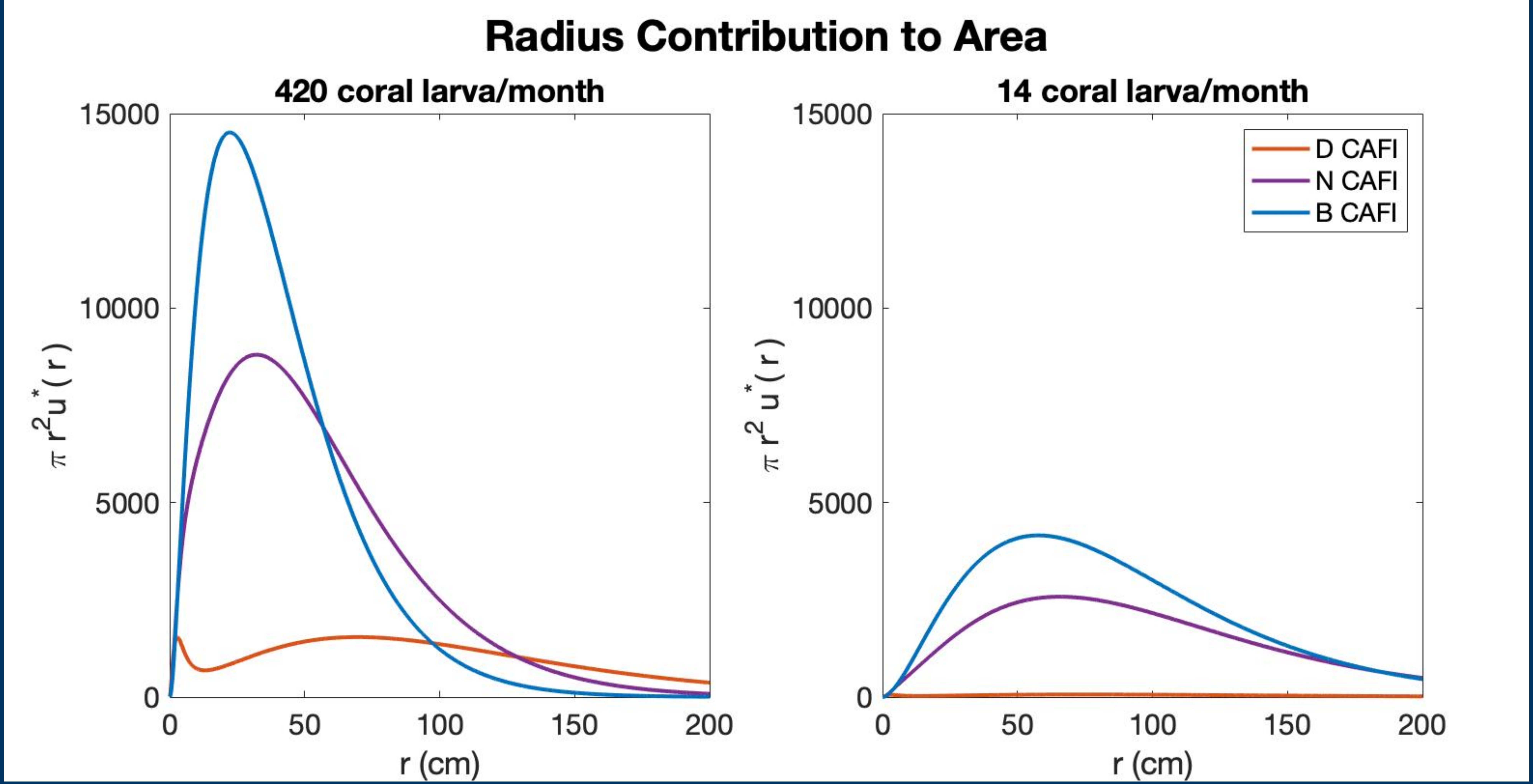
Visualizing the Size-What Corals do the eyes see?



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Deleterious CAFI Promote More Small and Large Corals

Biological intuition:

- If a coral survives deleterious CAFI, plenty room for growth
    - Corals either are small, or get rather large
- Beneficial CAFI help fill environment
    - Corals are all about 'medium' sized

- **Theorem:** *For $\phi_1 < \phi_2$ that admit $\bar{u}_1(r), \bar{u}_2(r)$ (where $A_1 < A_2$) then*

$$\lim_{r \to 0} \frac{\bar{u}_2(r)}{\bar{u}_1(r)} < 1 \text{ and } \lim_{r \to \infty} \frac{\bar{u}_2(r)}{\bar{u}_1(r)} < 1.$$

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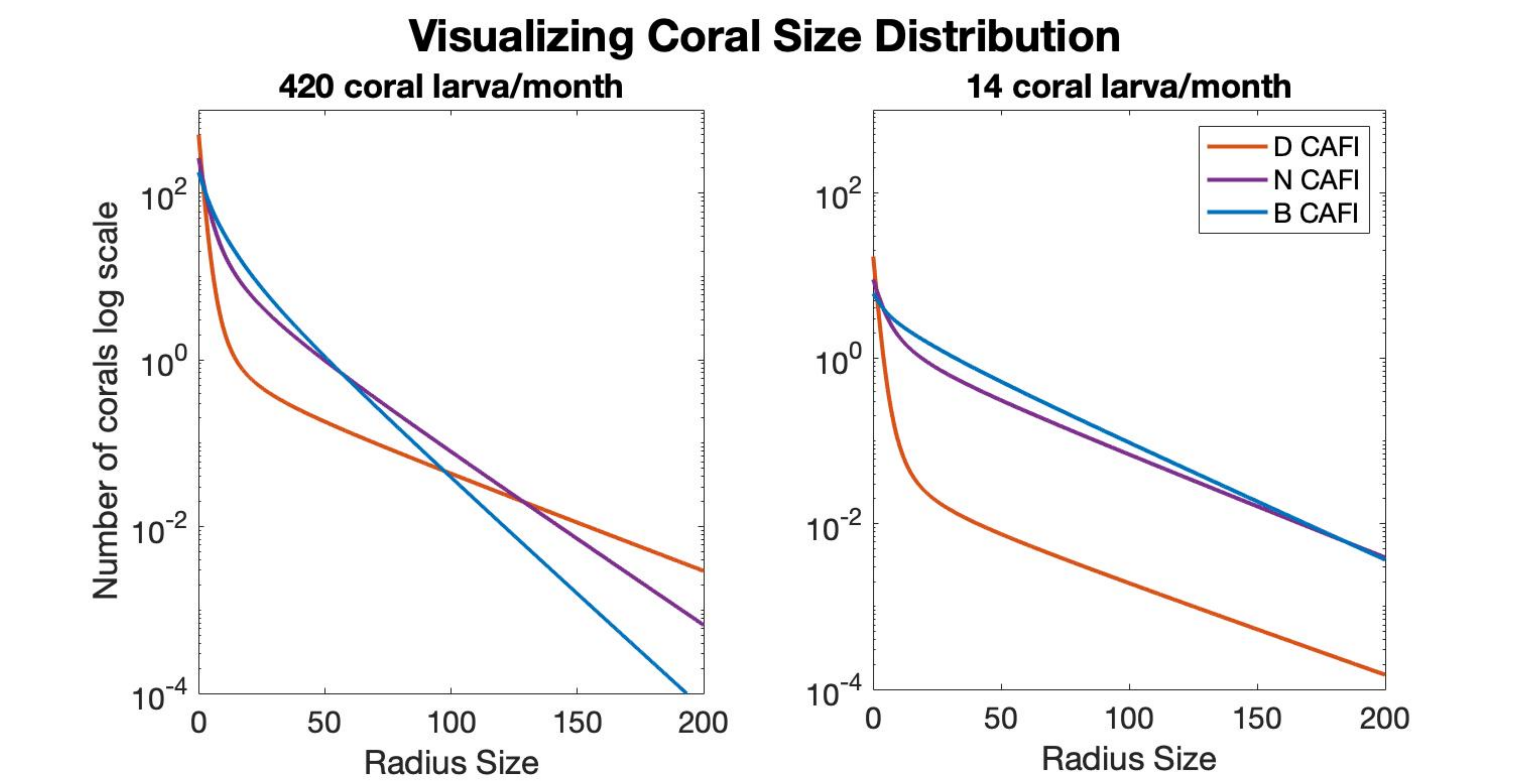

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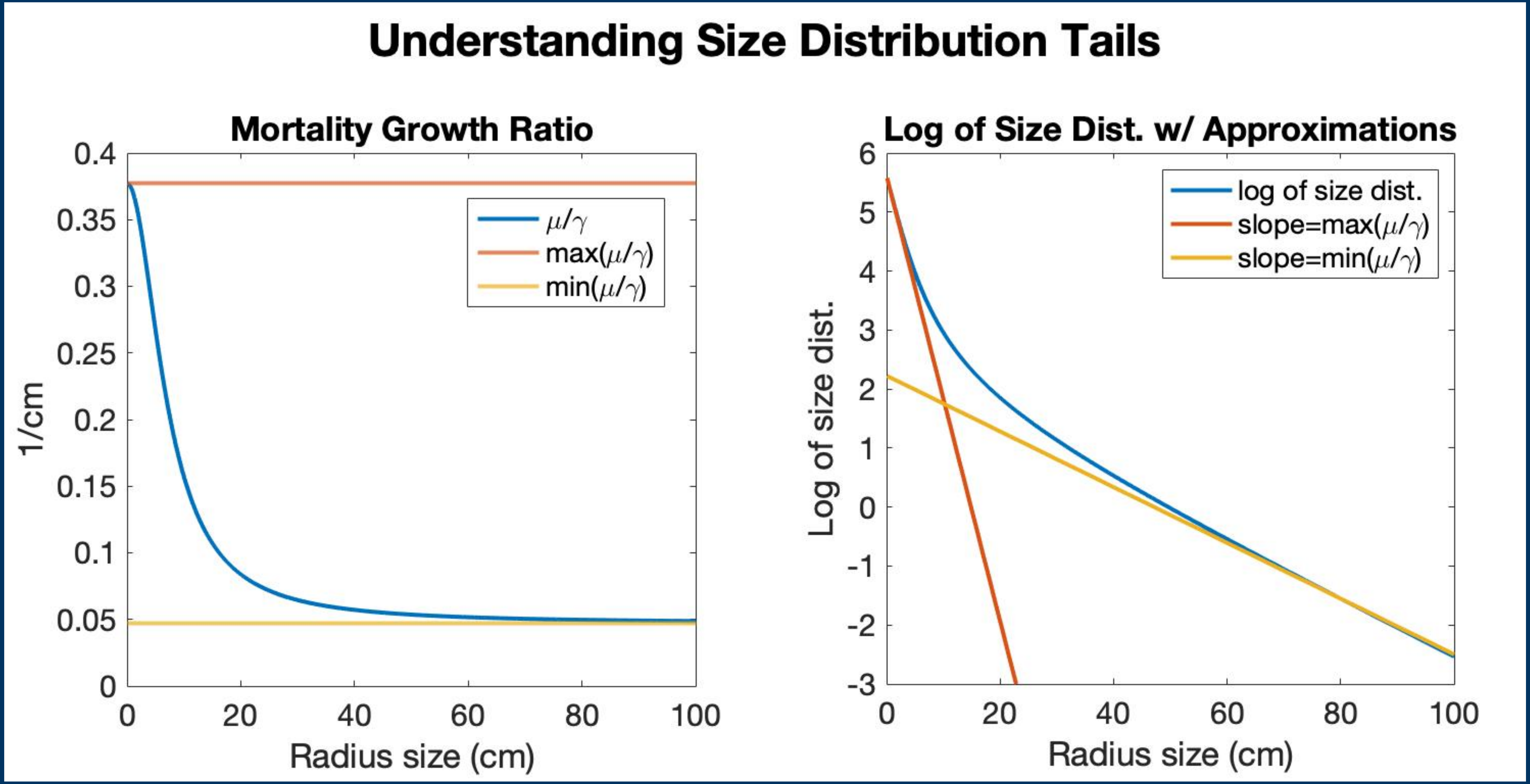

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Expected Maximum Coral

- By CAFI density definitions, we observe that for $r > r*$

$$\bar{u}(r) = C \exp\{-\nu r\} \text{ where } \nu = \min\left\{\mu(A, r)/\gamma(A, r)\right\}$$

- We can define a probability dist.

$$\Pr(R_i > r) = \frac{C}{||\bar{u}(r)||} \exp\{-\nu r\}$$

- Analytically derive expected max sized coral according to Gumble Distribution

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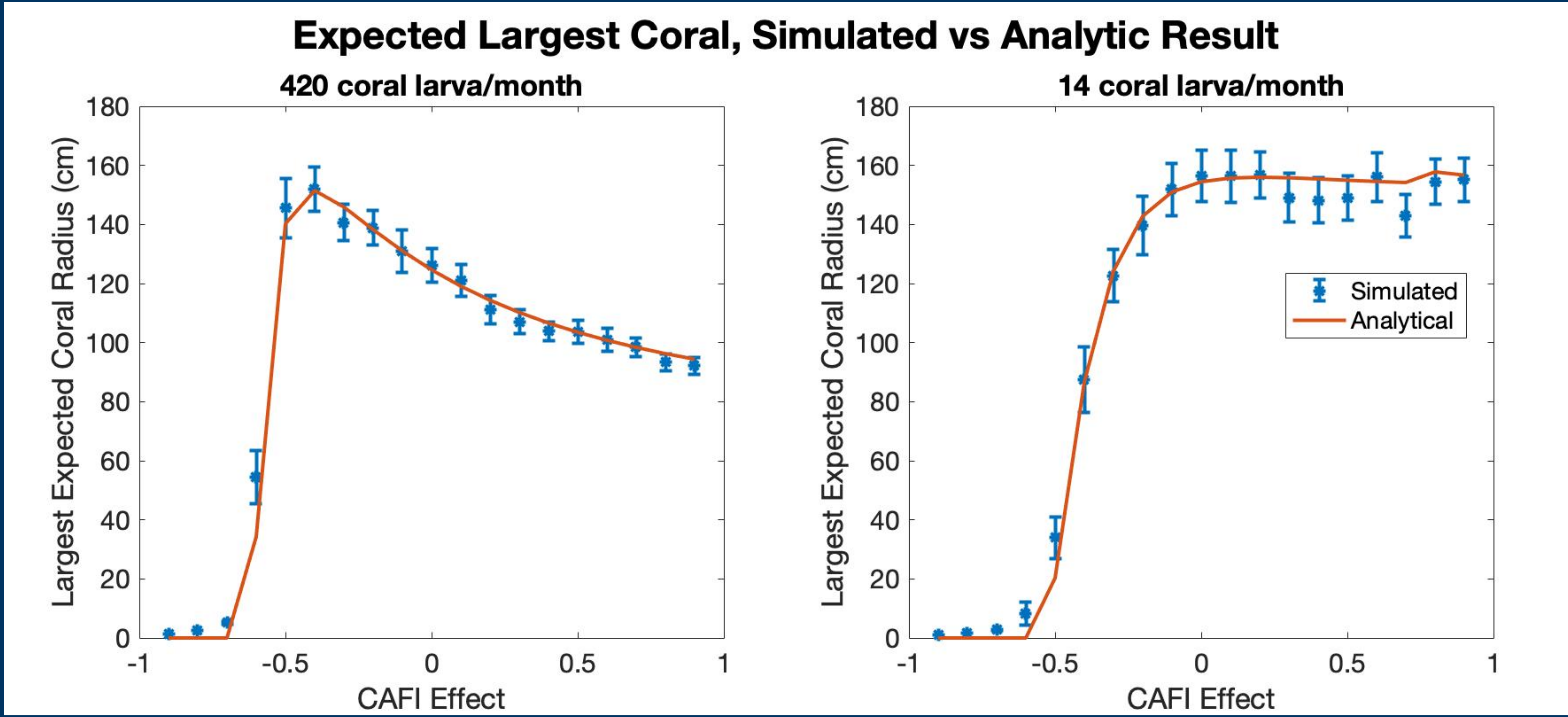
Expected Maximum Coral-Sampled vs Analytic



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Concluding Remarks

- Qualitative similarities to spatially explicit, 1-D stochastic model (Hamman)
    - Stochastic: Establish clustering patterns
    - Deterministic: Speed
- Unanwsered question: Analytically showing convergence of occupied area
    - limit point, no oscillations
- Extensions: Incorporating ‘disaster’ to analyze CAFI effect on regrowth

Thank you!