A cross-diffusion model for avoidance behavior in an intraguild predation community

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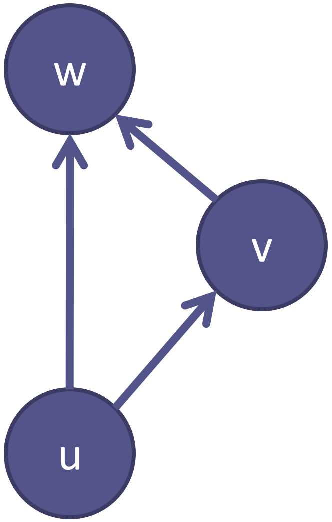
Intraguild Predation

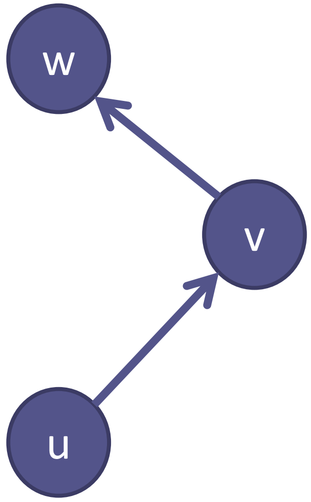
- 2 Species compete for a shared resource, and one preys on the other
- A mixture of competition and predator/prey dynamics
- Modeled with 3 species:

  IGPredator (w), IGPrey (v) and Resource (u)

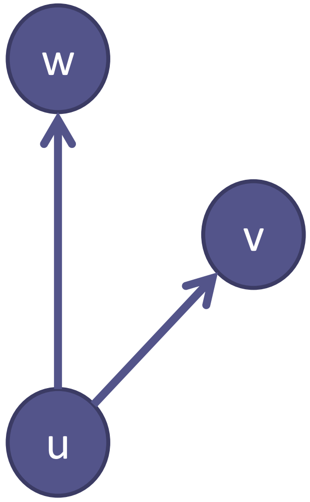


Three Modules In One

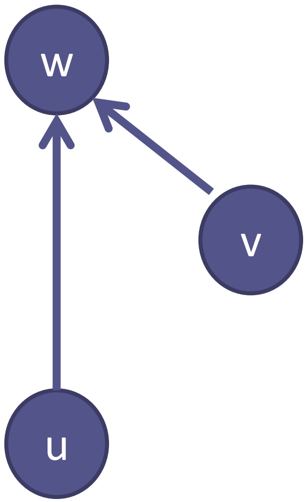
Linear Food Chain



Exploitative Competition



Apparent Competition



"A Theoretical Framework for Intraguild Predation"
R. Holt & G. Polis, American Naturalist, 1997

- Lotka-Volterra ODE model with 3 species and logistic resource
- Two necessary conditions for coexistence:
  1. the IGPrey is superior at exploiting the resource
  2. the IGPredator gains sufficiently from consumption of the IGPrey
- Coexistence most likely at intermediate resource productivity
- Alternative stable states possible

“A Theoretical Framework for Intraguild Predation” (cont.)

- Further mechanisms for promoting coexistence in IGP systems were postulated:

1. Age or stage structure (Mylius et al, Am. Nat. 2001)
2. Adaptive behaviors, e.g. prey switching, prey vigilance (Kimbrell, Holt, Lundberg, JTB 2007)
3. Spatial Heterogeneity (Amarasekare, Am. Nat. 2007)
4. Additional Species (full food web models)

Interspecific Killing

- Similar to IGP with one key difference: the killer species does not consume the victim
- Holt & Polis' model predicts that coexistence of competitors with interspecific killing should not happen
- Present in many mammalian interactions

Avoidance Behaviors of IGPrey

- Many ecological studies of IGP systems have found that the IGPrey utilizes avoidance behaviors:
  - cheetahs & lions (and hyenas)
  - tawny owls & eagle owls
  - black kites & eagle owls
  - lady beetles & lacewing
  - mongoose and genets & Iberian Lynx
  - swift foxes & coyotes
  - “big” scorpions and “little” scorpions

Avoiding What?

- Ecological studies suggest two different mechanisms:
  1. avoid predation risk
  2. avoid areas with bad resource/predation risk trade-off

- Avoiding predation risk can backfire.

- If resources are abundant or IGPredator is very aggressive, it is difficult to determine which is being observed.

A Cross-Diffusion Model for IGPrey Avoidance

ASSUMPTIONS:

- IGPrey is able to assess local resource availability and predation risk
- IGPrey follows a random walk where probability of departure is proportional to a function of **local** resource and IGPredator density
- IGPredator and resource disperse randomly (pure diffusion)

The Model Equations

$$\frac{\partial u}{\partial t} = d_1 \Delta u + f(x,u,v,w)\, u$$
$$\frac{\partial v}{\partial t} = \Delta\left[M(u,w)v\right] + g(u,v,w)\, v \qquad \text{in } \Omega \text{ and Neumann B.C.'s on } \partial\Omega$$
$$\frac{\partial w}{\partial t} = d_3 \Delta w + h(u,v,w)\, w$$

and $$f(x,u,v,w) = r(x) - \omega_1 u - \frac{a_1 v}{1 + h_1 a_1 u} - \frac{a_2 w}{1 + h_2 a_2 u + h_3 a_3 v}$$

$$g(u,v,w) = \frac{e_1 a_1 u}{1 + h_1 a_1 u} - \frac{a_3 w}{1 + a_2 h_2 u + h_3 a_3 v} - \mu_1 - \omega_2 v$$

$$h(u,v,w) = \frac{e_2 a_2 u + e_2 a_3 v}{1 + a_2 h_2 u + a_3 h_3 v} - \mu_2 - \omega_3 w$$

Fitness Dependent Avoidance

- Want M(u,w) to be a function of IGPrey fitness, g(u, v, w)
- Use g*(u, w) = g(u, 0, w) instead (fitness when rare)
- M should be higher when g* < 0
- Tunable parameter λ reflecting strength of avoidance

1. $M_\lambda(g^*) \leq d_2$ for $g^* \geq 0$,
2. $\lim_{\lambda\to\infty} M_\lambda(g^*) = \infty$ for $g^* < 0$,
3. $M_\lambda(g^*) \geq d > 0$ for all g^*,
4. $M_\lambda(g^*)$ twice differentiable.

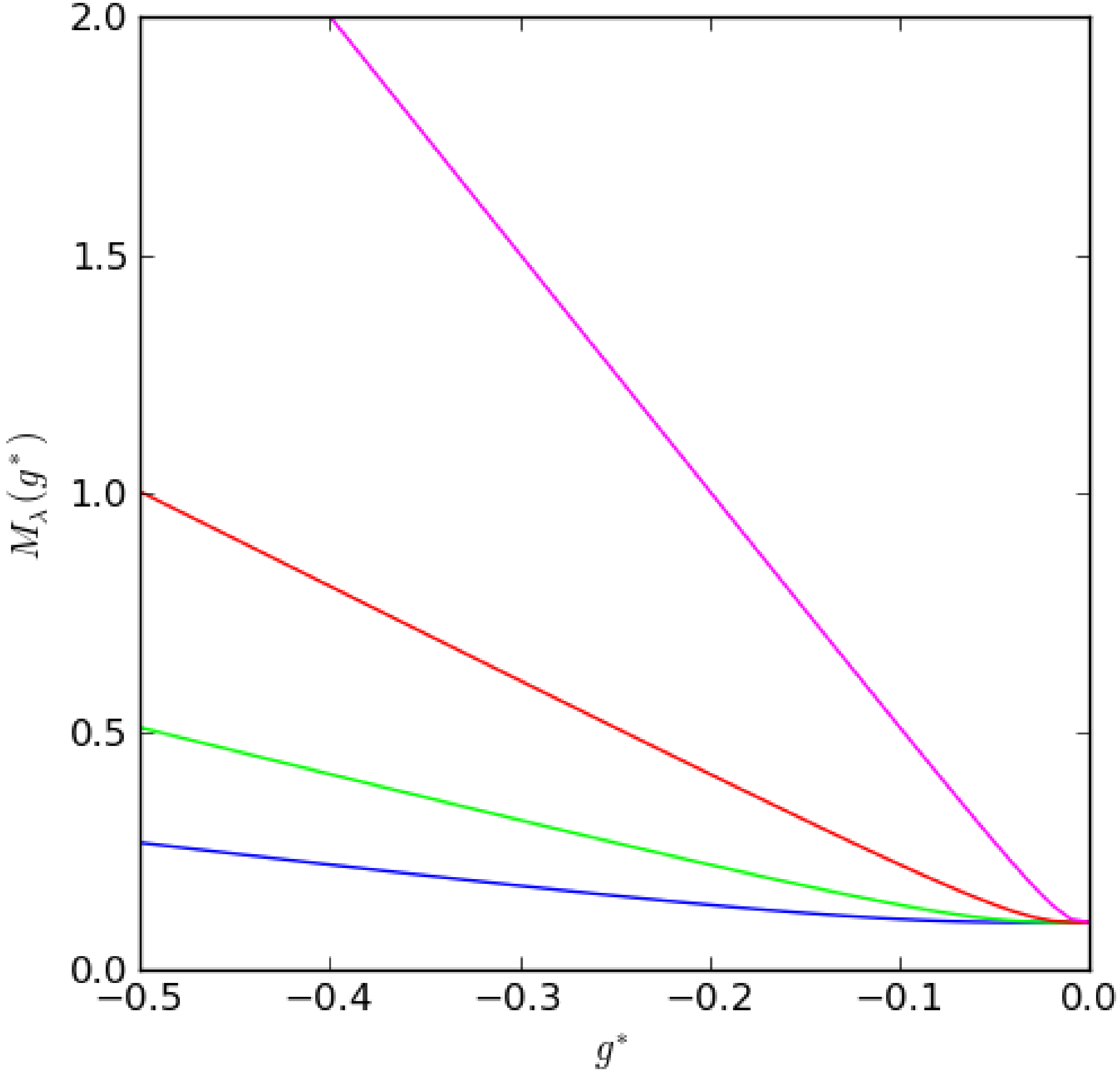
Example for M(g*)

One choice of $M(g^*)$ that would reflect a tendancy to avoid "bad areas" would be

$$M_\lambda(g^*) = \begin{cases} d_2 & \text{if } g^* \geq 0, \\ -\lambda g^* + d_2 & \text{if } g^* < 0, \end{cases}$$

but this is not differentialbe at $g^* = 0$. Instead, we can use

$$M_\lambda(g^*) = \begin{cases} d_2 & \text{if } g^* \geq 0, \\ -\lambda g^* e^{\frac{-d_2}{(\lambda g^*)}} + d_2 & \text{if } g^* < 0. \end{cases}$$



2.0
1.5
1.0
0.5
0.0
−0.5
−0.4
−0.3
−0.2
−0.1
0.0
$M_\lambda(g^*)$
g^*

Triangular Systems

Consider the system:

$$\frac{\partial \vec{u}}{\partial t} = \nabla \cdot (\mathbf{A}(x, \vec{u}) \nabla \vec{u}) + \vec{f}(x, \vec{u}, \nabla \vec{u})$$

where the derivatives are applied component-wise. We say this system is triangular if

$$\mathbf{A}(x, \vec{u}) = (a_{ij}(x, \vec{u})) \ \text{ with } a_{ij} = 0 \text{ if } j < i.$$

If $\mathbf{A}$ is triangular and normally elliptic and $\vec{f}$ is affine in $\nabla \vec{u}$, then solutions will be classical global solutions if their L_∞ norms remain bounded. (Amann '90)

Global Existence and the Compact Attractor

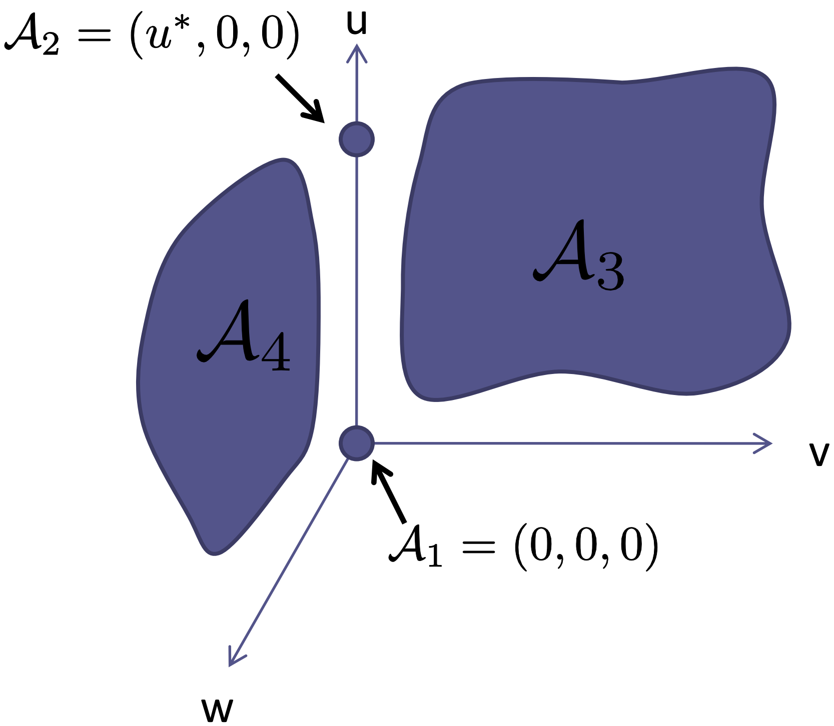
- With a few extra conditions on $\mathbf{A}$ and $\vec{f}$, if $\|u\|_\infty$, $\|w\|_\infty$ and $\|v\|_2$ are ultimately uniformly bounded, then solutions exist globally *and* there is a compact attractor in $W^{1,p}(\Omega)$ for $p > n$. (Le 2003)
- Only having to deal with $\|v\|_2$ instead of $\|v\|_\infty$ is critical!
- The compact attractor allows us to apply permanence theory which is also a big win.
- The bound on v should actually be the L_n-norm where n is the dimension of the domain.

Outline of Existence Proof

- $\|u\|_\infty$ and $\|w\|_\infty$ bounds are easy
- $\|v\|_2$ bound comes from multiple applications of Gagliardo-Nirenberg inequalities and Uniform Gronwall Lemma.
- Along the way, a bound on $\int_t^{t+1} \|\nabla u(s)\|_4^4 \, ds$ is needed, which is in turn bounded by quantities involving $\int_t^{t+1} \left\| \frac{\partial u}{\partial t} \right\|_2^2 ds$ and $\int_t^{t+1} \|\Delta u\|_2^2 \, ds$ (and the same for w).

Boundary Attractors

- (0,0,0) is an equilibrium that attracts all data in the u=0 plane
- $(u^*, 0, 0)$ is the unique positive equilibrium to the resource only subsystem
- If v can invade $(u^*, 0, 0)$, then there is an attractor $\mathcal{A}_3$ in the w=0 plane that is bounded away from the axes
- If w can invade $(u^*, 0, 0)$, then there is an attractor $\mathcal{A}_4$ in the v=0 plane that is bounded away from the axes
- No subset of these can form a chain



Consequences of Strong Avoidance

Theorem:
Suppose there exists a $x \in \Omega$ such that $g^*(u(x), w(x)) > 0$ for all $(u, w) \in \mathcal{A}_4$, then there is a $C > 0$ such that the IGPrey will be uniformly persistent for any $\lambda \geq C$.

Sketch of Proof

- Set $\xi_\lambda(x) = \min_{(u,w)\in\mathcal{A}_4} \frac{g^*(u(x),w(x))}{M_\lambda(g^*(u(x),w(x)))}$

- Show that for sufficiently large λ the principal eigenvalue, σ, of

$$\Delta\psi + \xi_\lambda(x)\psi = \sigma\psi \text{ in } \Omega \text{ and } \frac{\partial\psi}{\partial n} = 0 \text{ on } \partial\Omega$$

  is positive.

- Use this to prove $W^S(\mathcal{A}_4 \cap (X \setminus S) = \emptyset$.

- Deconstruct proof of Acyclicity Theorem to get statement about persistence of v.

A Contrast With Slow Diffusion

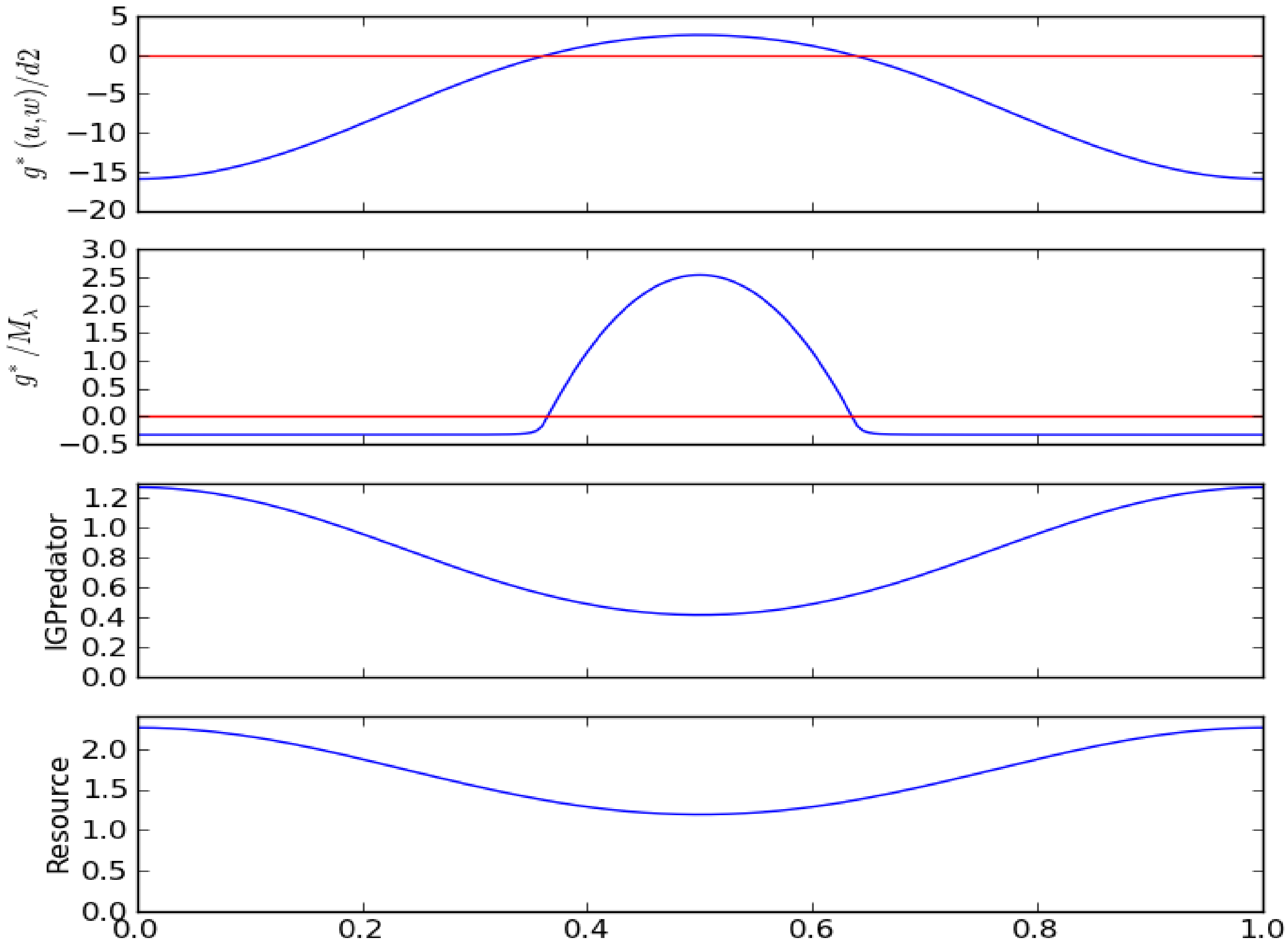
- It is well known that the same result holds for small pure diffusion. This really operates on the virtue of **low motility in "good areas".**

- The result presented herein corresponds to **high motility in "bad areas".**

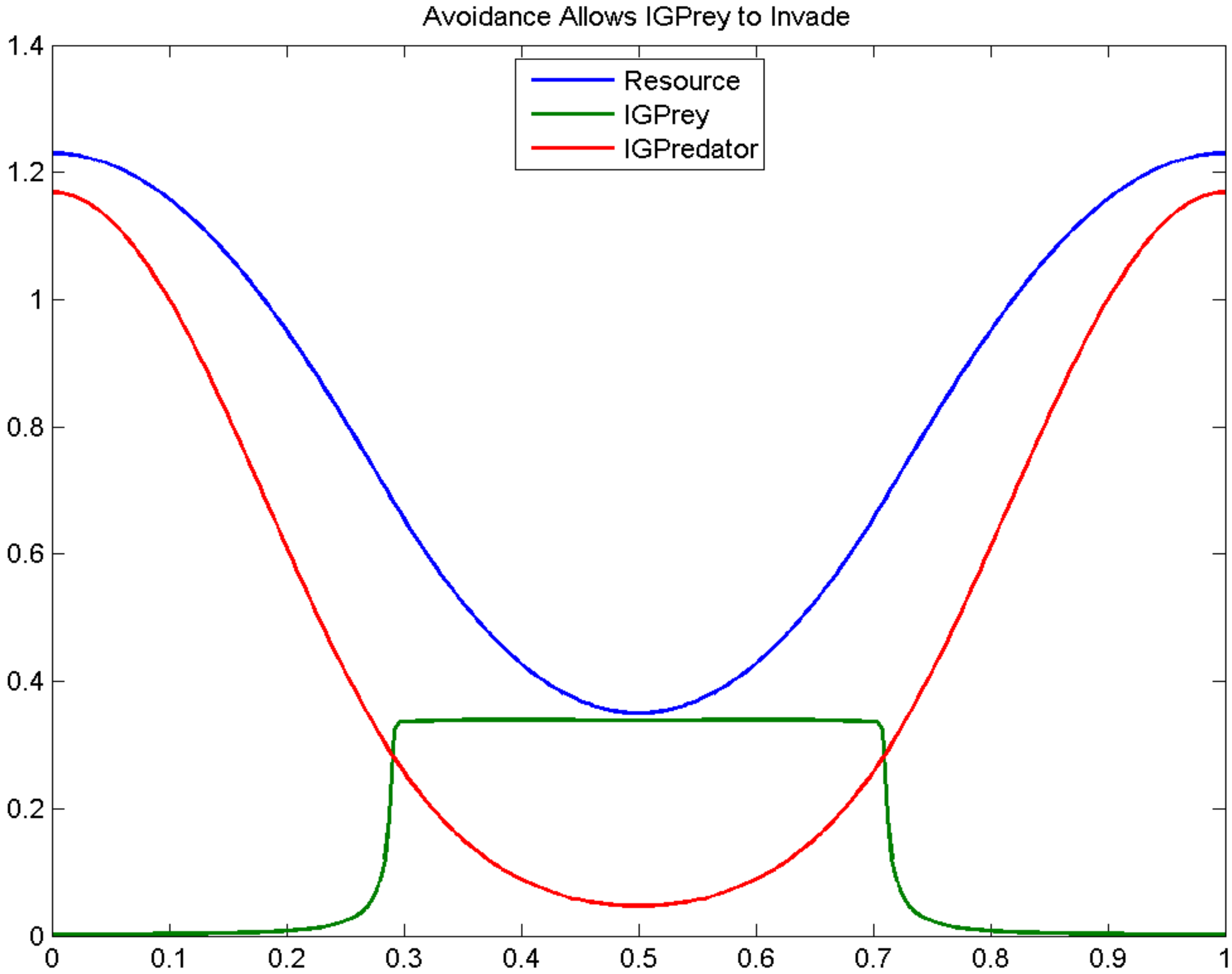
- Either mechanism can lead to persistence; but, they have very different ecological interpretations.

- Combining strategies would be even better.

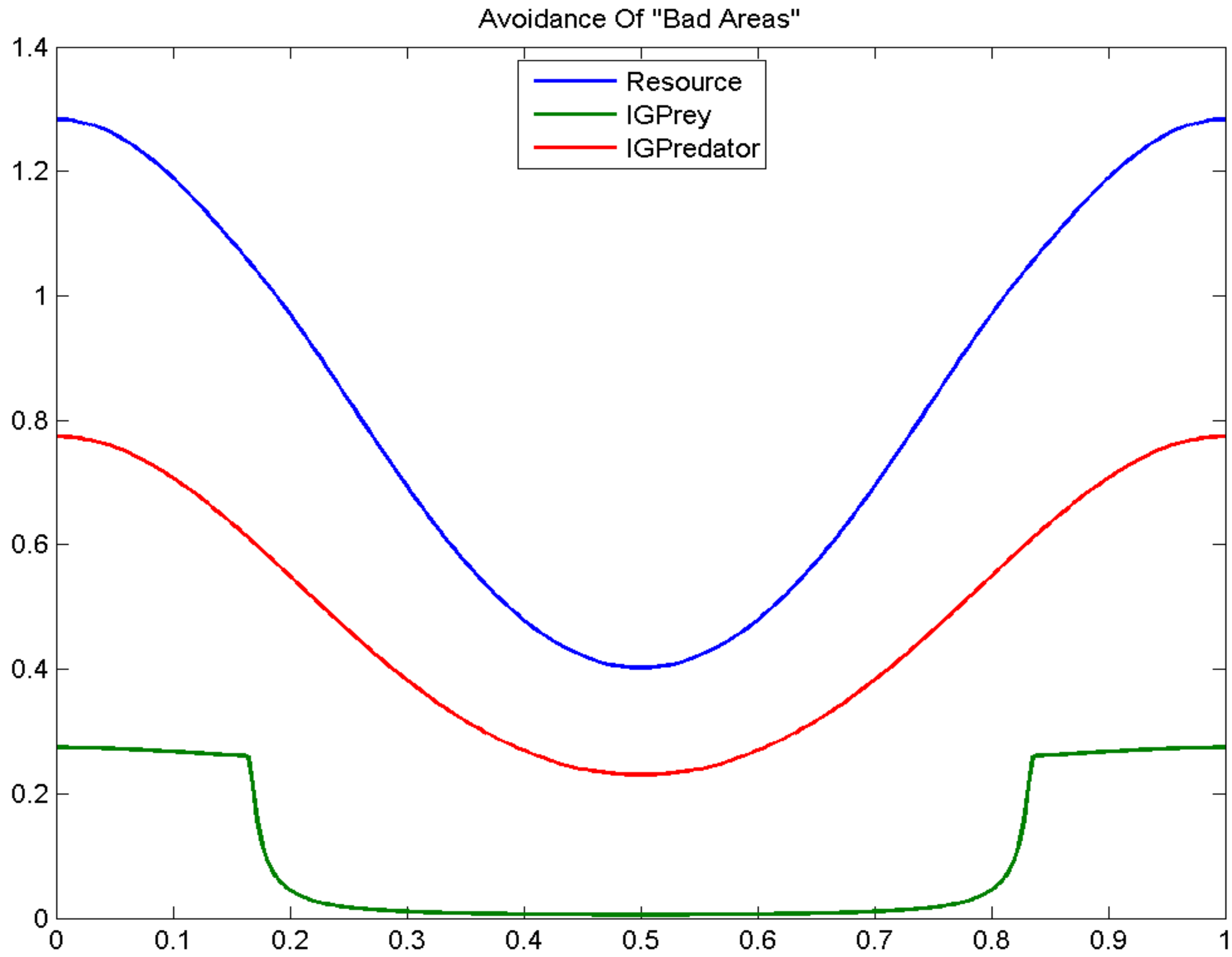
u-w Equilibrium With Small Region where $g^* > 0$



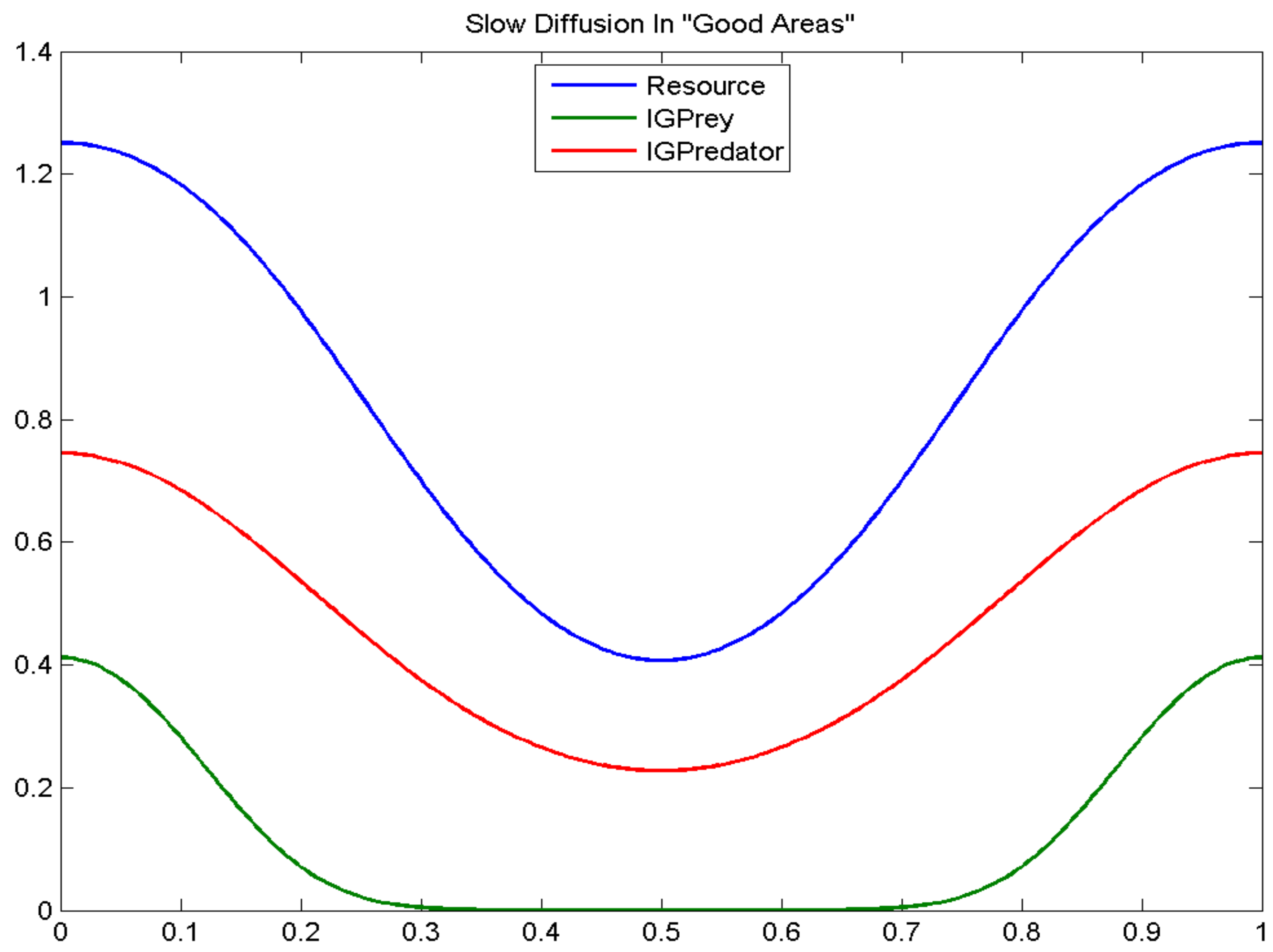
Coexistence By Segregation



IGPrey Coexisting with Superior Competitor IGPredator Through Use of Avoidance Strategy



Coexistence By Slow Diffusion



Key Points

- High motility in areas of negative fitness can have the same types of effects on principal eigenvalues (invasion fitness) as low motility in areas of positive fitness.

- In IGP communities, fitness based avoidance strategies for the IGPrey can lead to more robust coexistence states.

- In particular, in the case of aggressive IGPredators, the IGPredators will monopolize areas with higher resources and the IGPrey will be marginalized to areas with lower resources (but less predators). This results in coexistence by segregation.

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