Counterintuitive patterns of dispersal evolution in a simple trophic metacommunity

Pradeep Pillai,
Marine Science Center,
Northeastern University

Everything Disperses to Miami,
University of Miami Coral Gables
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Evolution of dispersal in metapopulation

- Ecologically: Dispersal important for maintaining a species in a spatially subdivided population.
- Evolutionarily: Dispersal comes at a cost of decreasing local fitness.

Evolution of dispersal in a metacommunity

- What selection pressures exist on species dispersal rates at the metacommunity level?
- Dispersal repeatedly shown to increase with local extinction rate in metapopulations
  - Van Valen (1971), Levin and Olivieri (1984), Comins et al. (1981), Olivieri et al. (1995)

Research Question

- Want to measure how evolutionary stable (ESS) dispersal will change with increasing extinction rates caused by unstable interaction between a prey and predator

Evolution of dispersal

Background theory:

Importance of dispersal

- Eg. Huffaker, 1958

T. occidantelis

E. sexmaculatus

Evolution of dispersal

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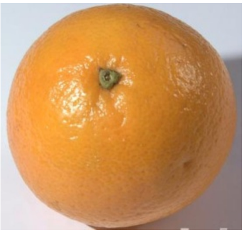

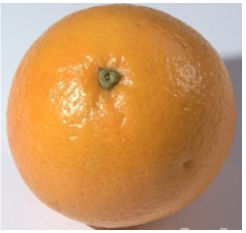

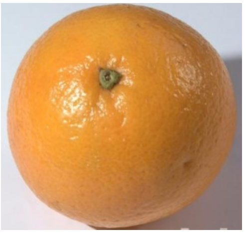

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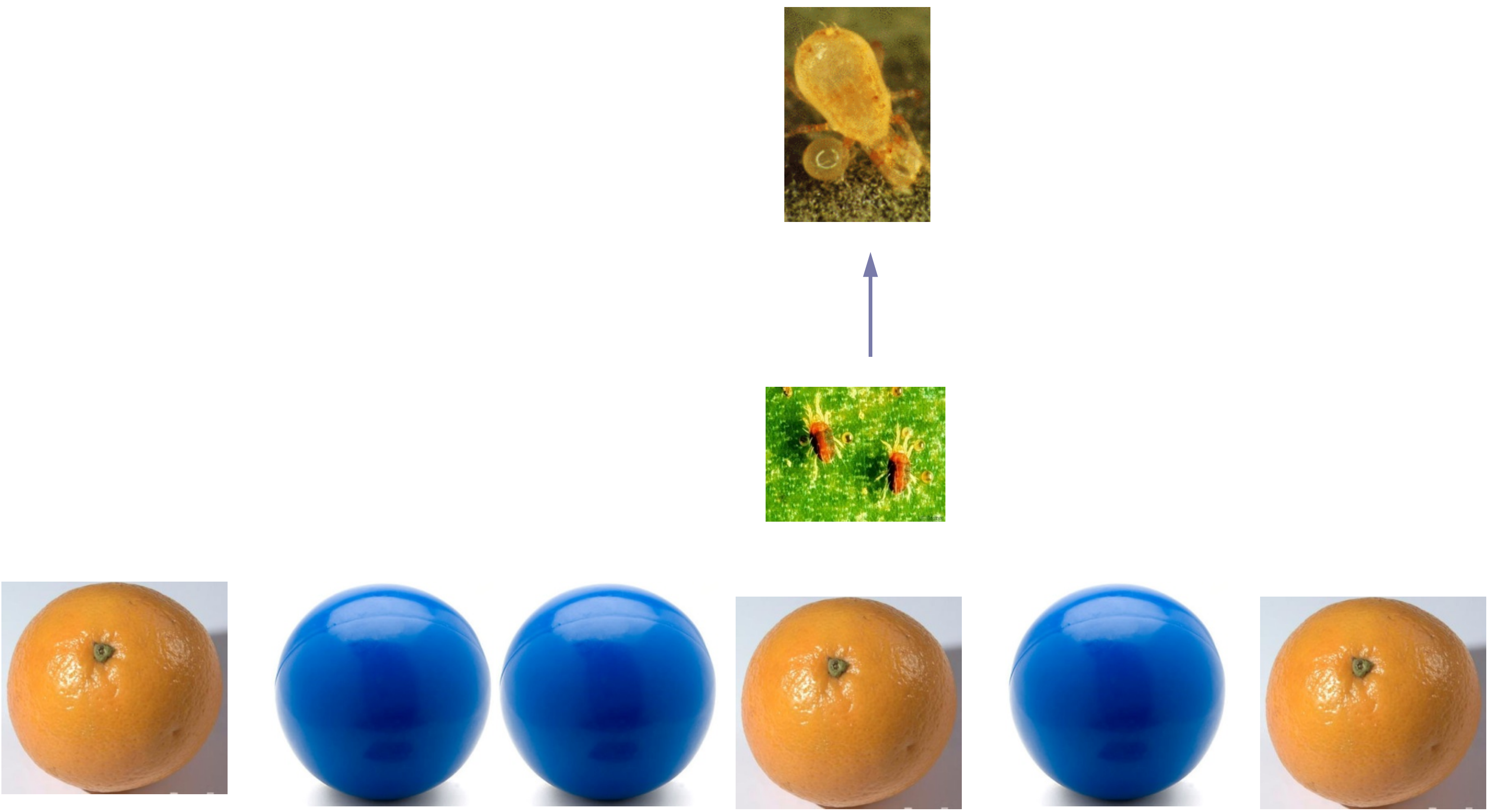

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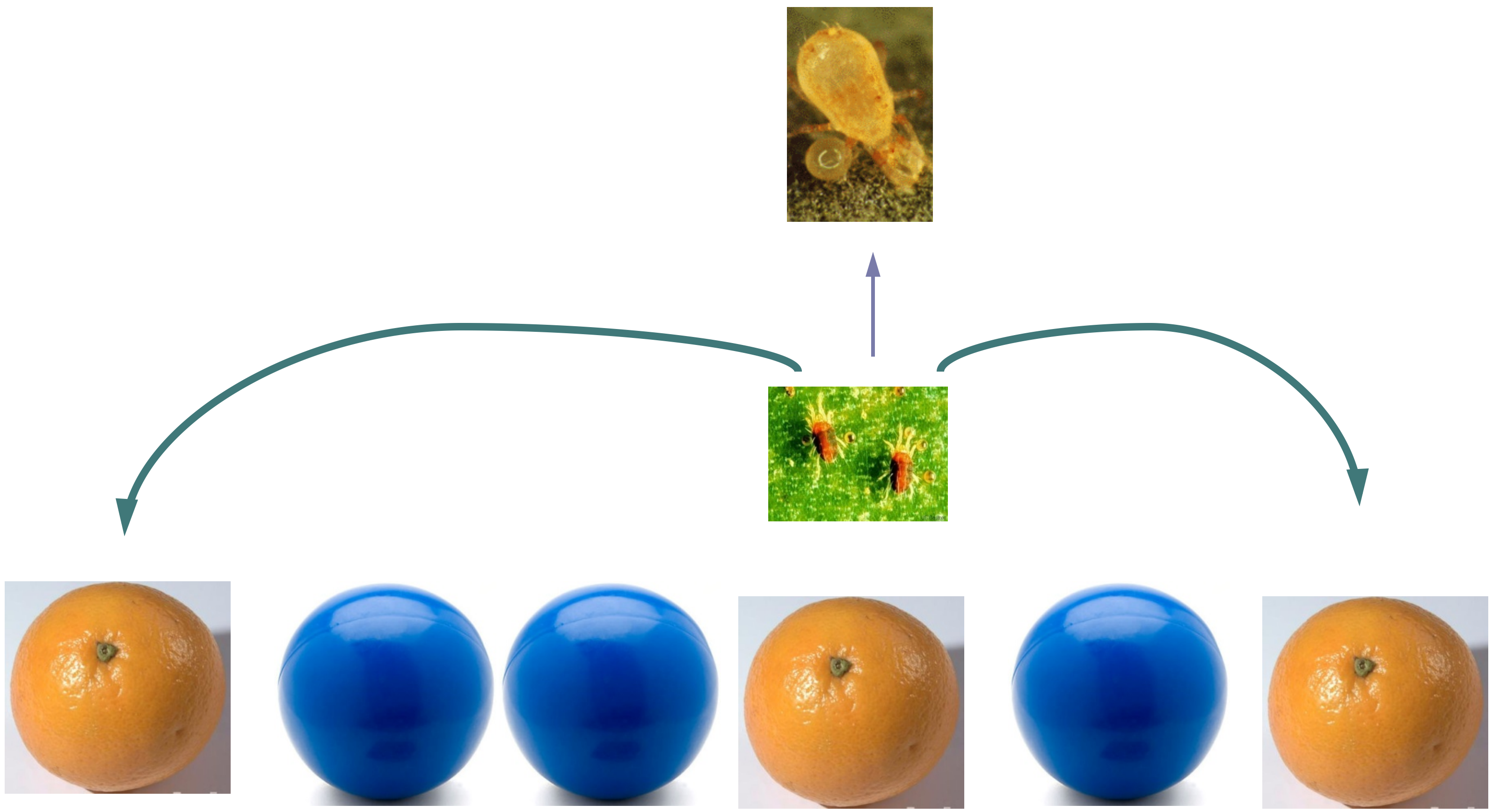

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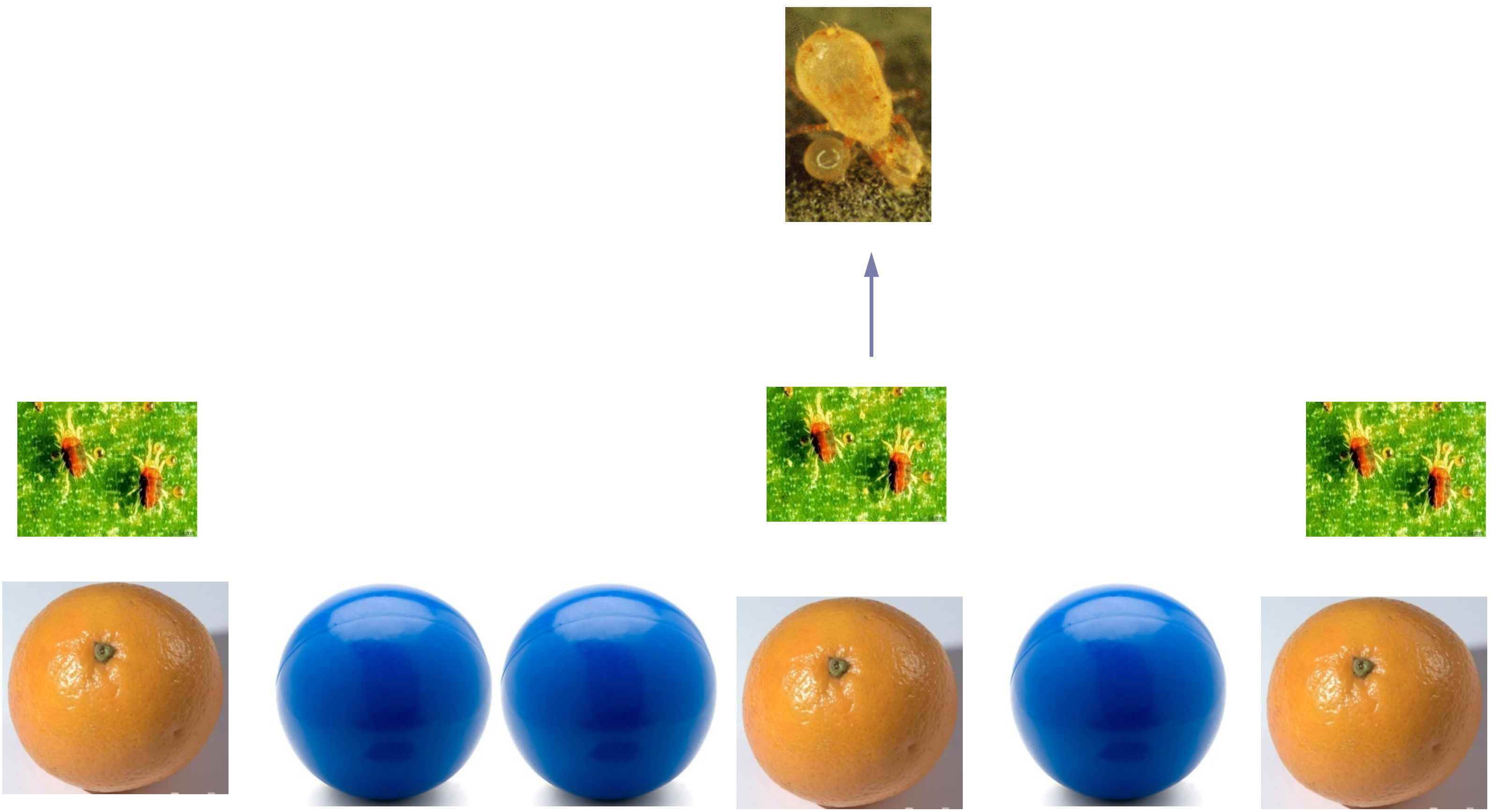

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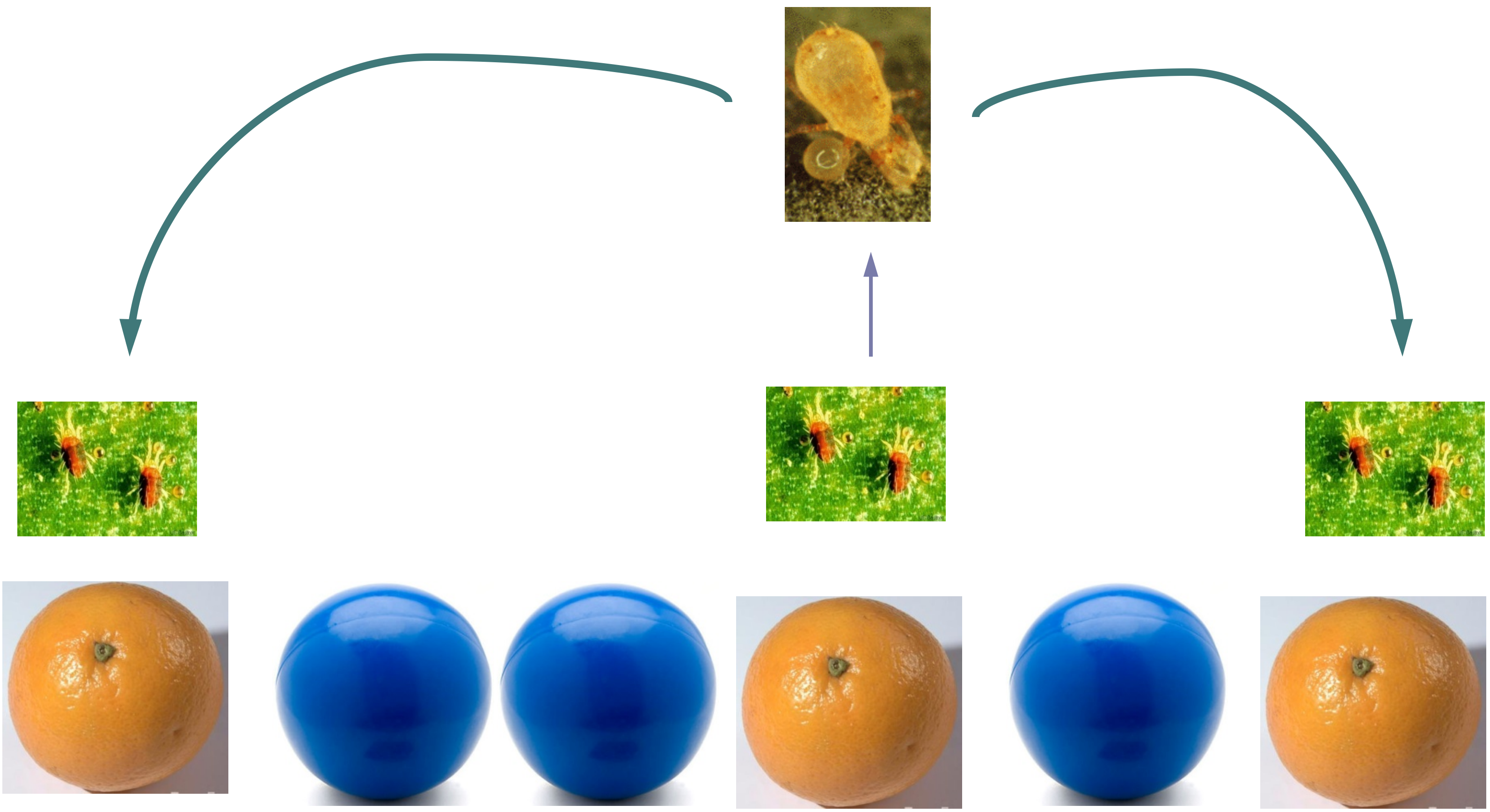

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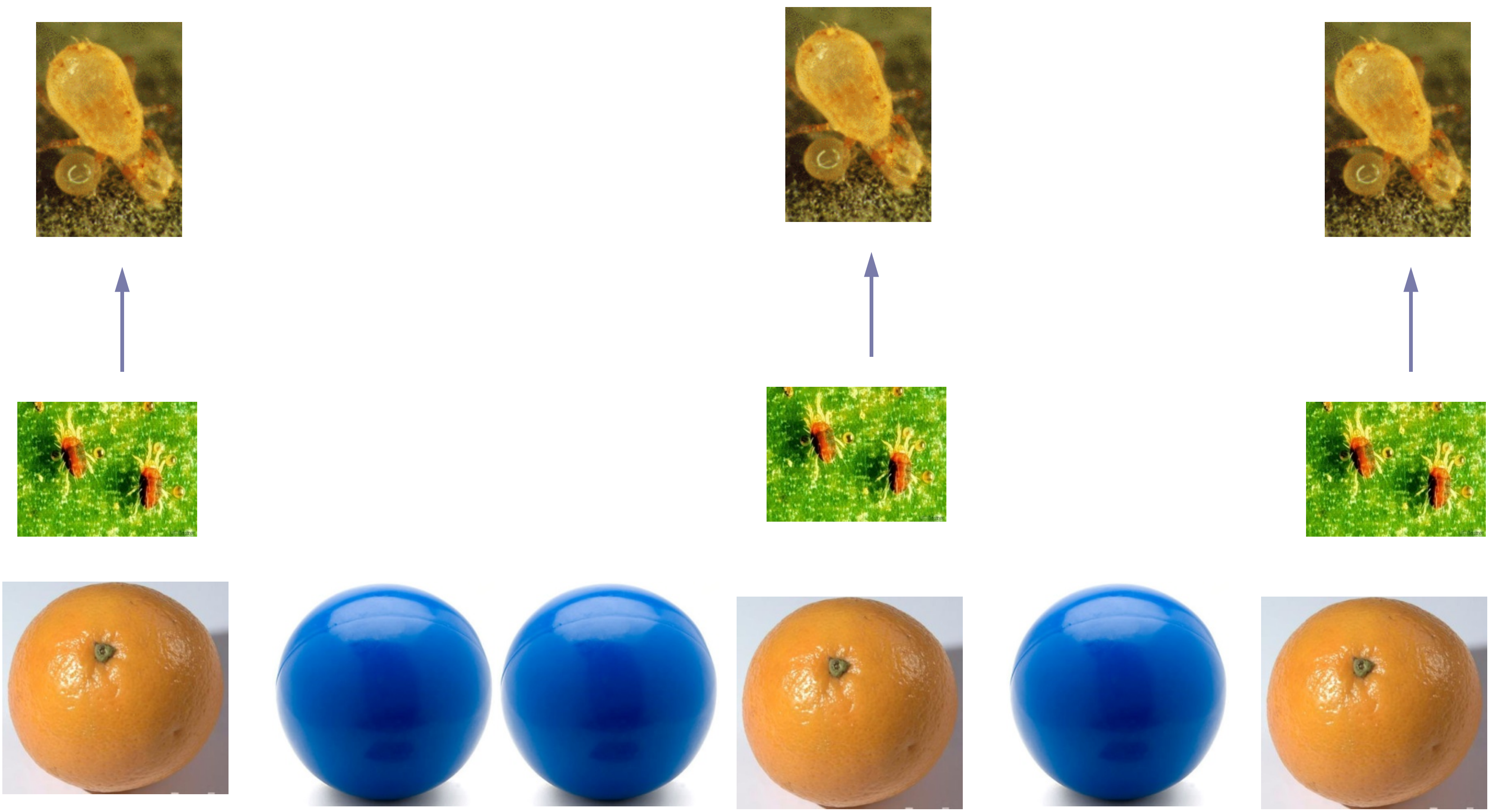

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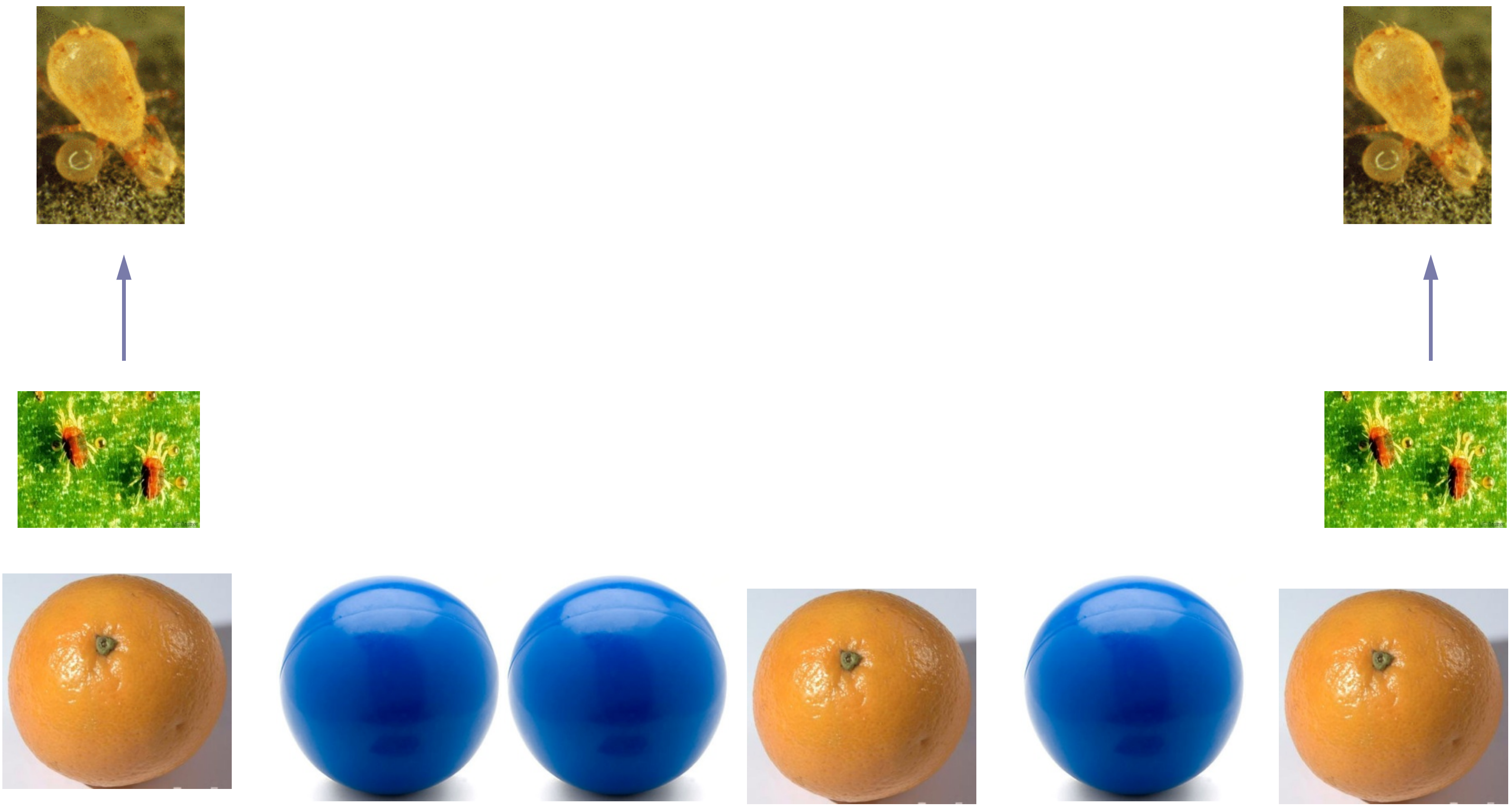


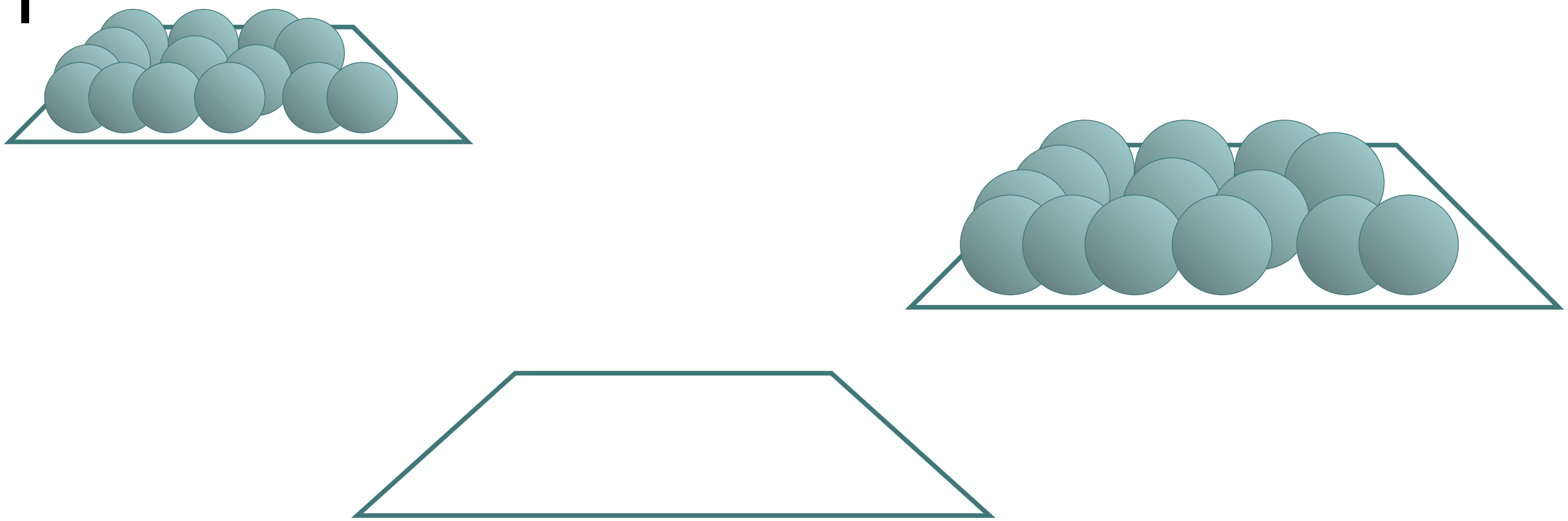
Evolution of dispersal

Metacommunity framework for studying dispersal evolution

- Use a patch-dynamic metacommunity approach to model spatially structured populations of interacting predator and prey species.

Evolution of dispersal

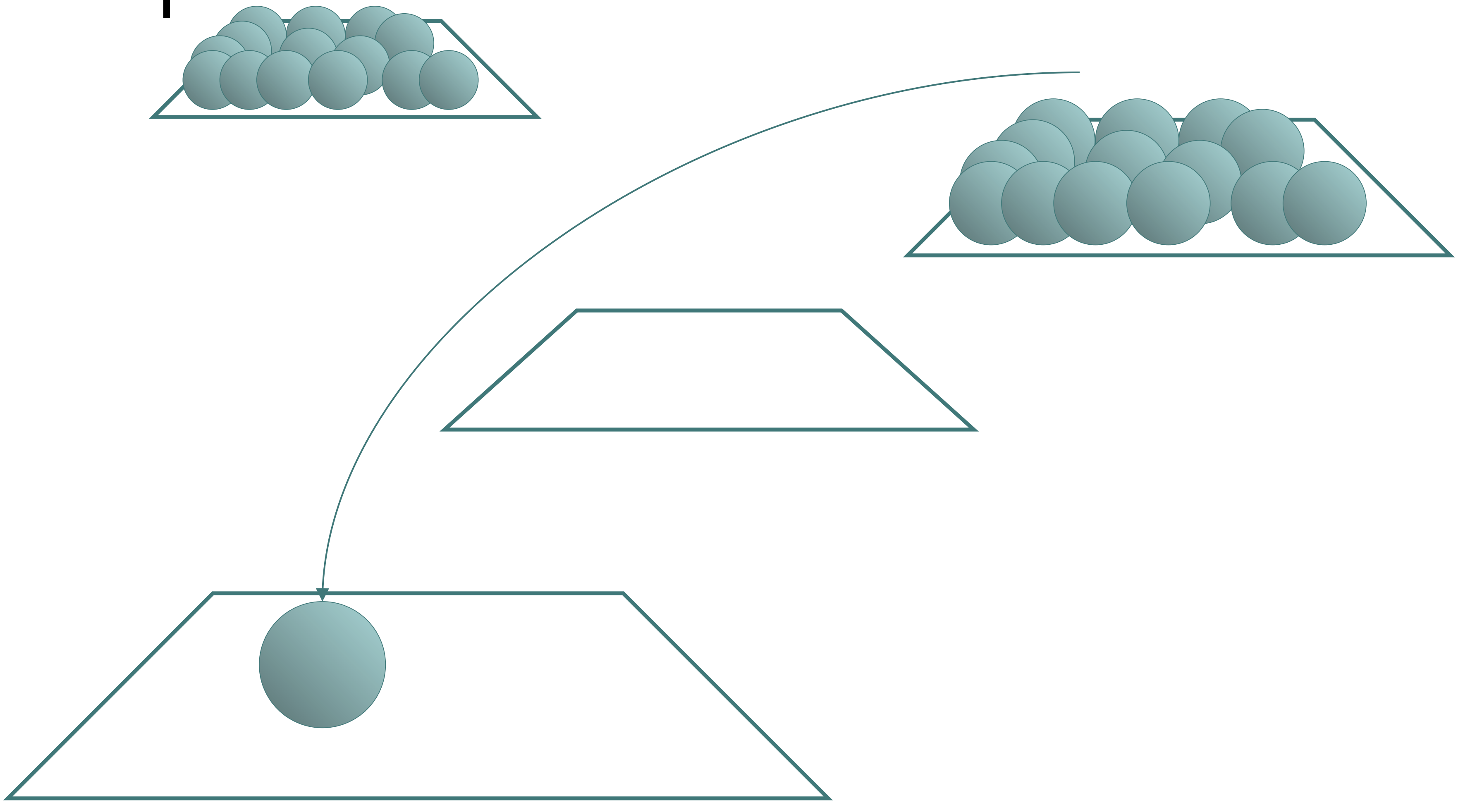
Metapopulation dynamics



"**population of populations** which go extinct locally and recolonize." (Levins 1970)

Evolution of dispersal

Metapopulation dynamics



Evolution of dispersal

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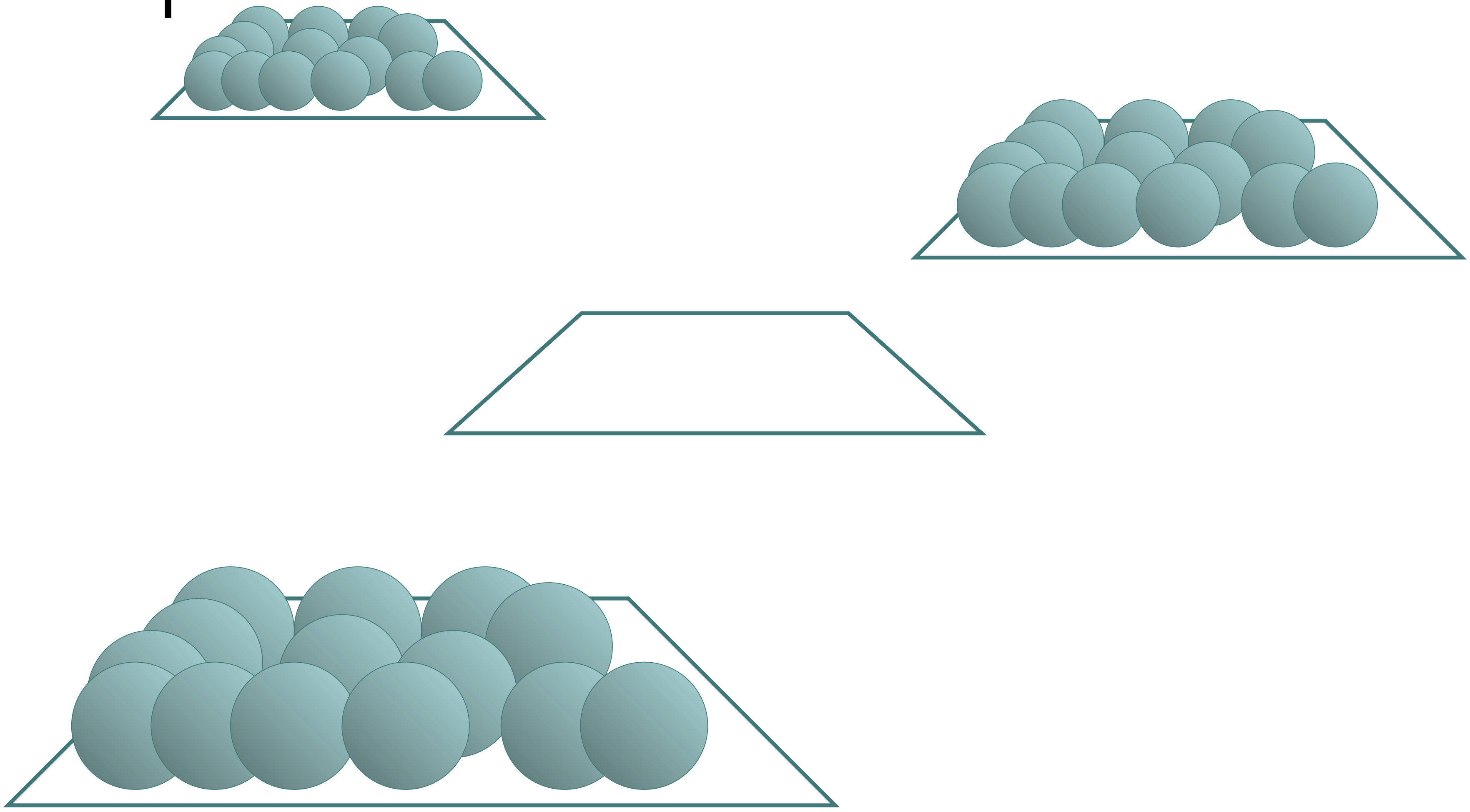
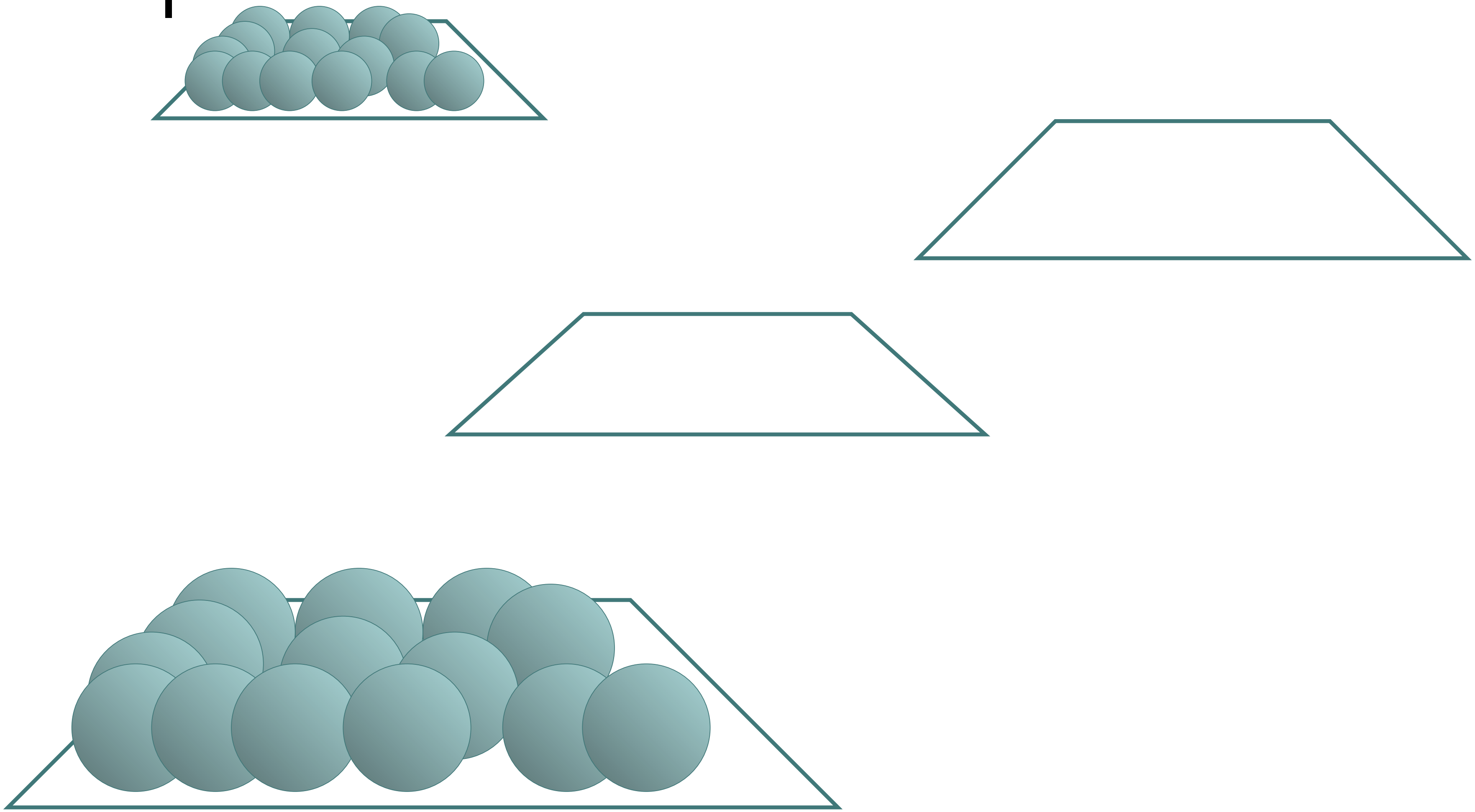


Evolution of dispersal

Metapopulation dynamics



Evolution of dispersal

Metapopulation dynamics

$$\frac{\mathrm{d}p}{\mathrm{d}t} = \text{Colonization of new patches} - \text{local Extinction in occupied patches}$$

Metapopulation dynamics

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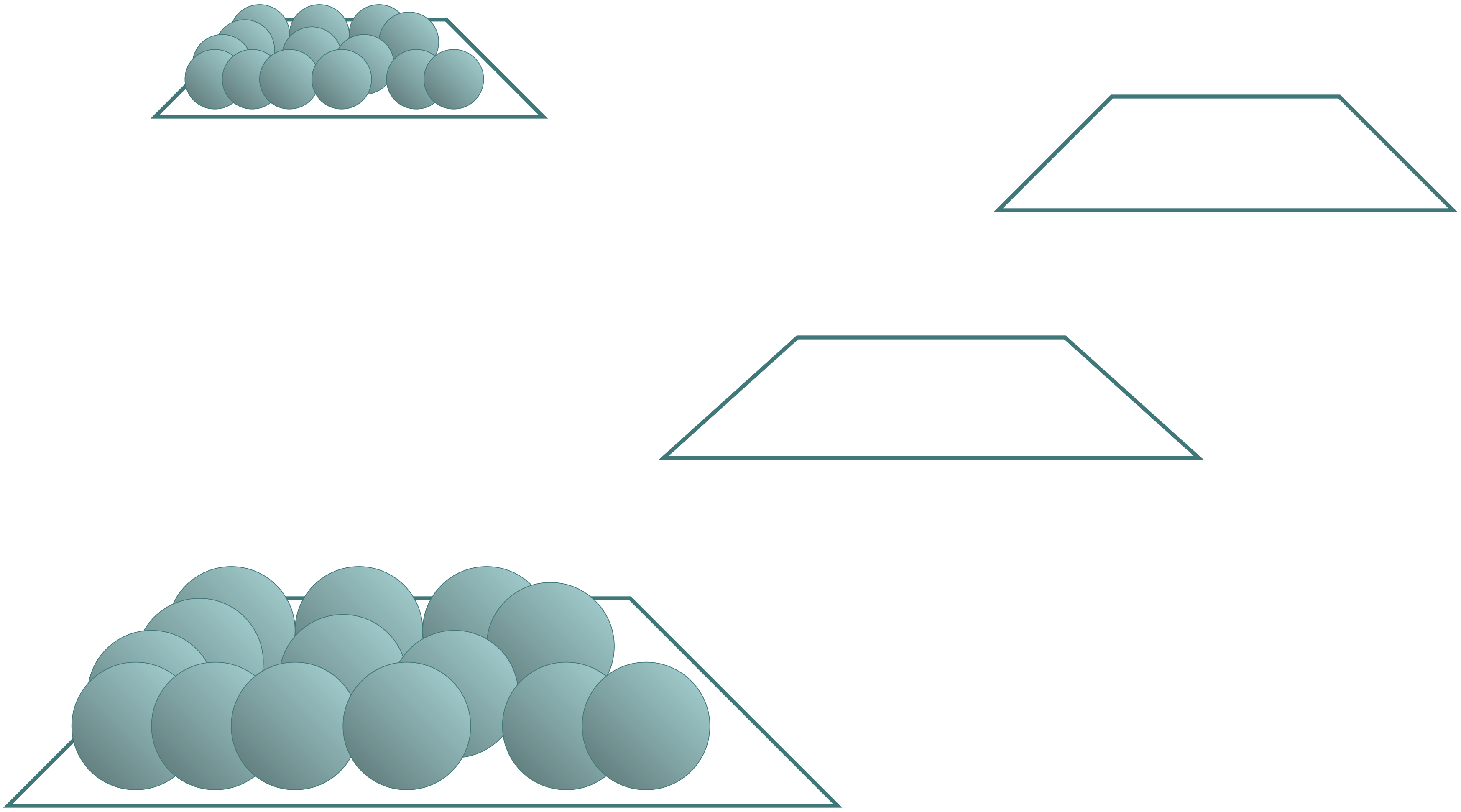
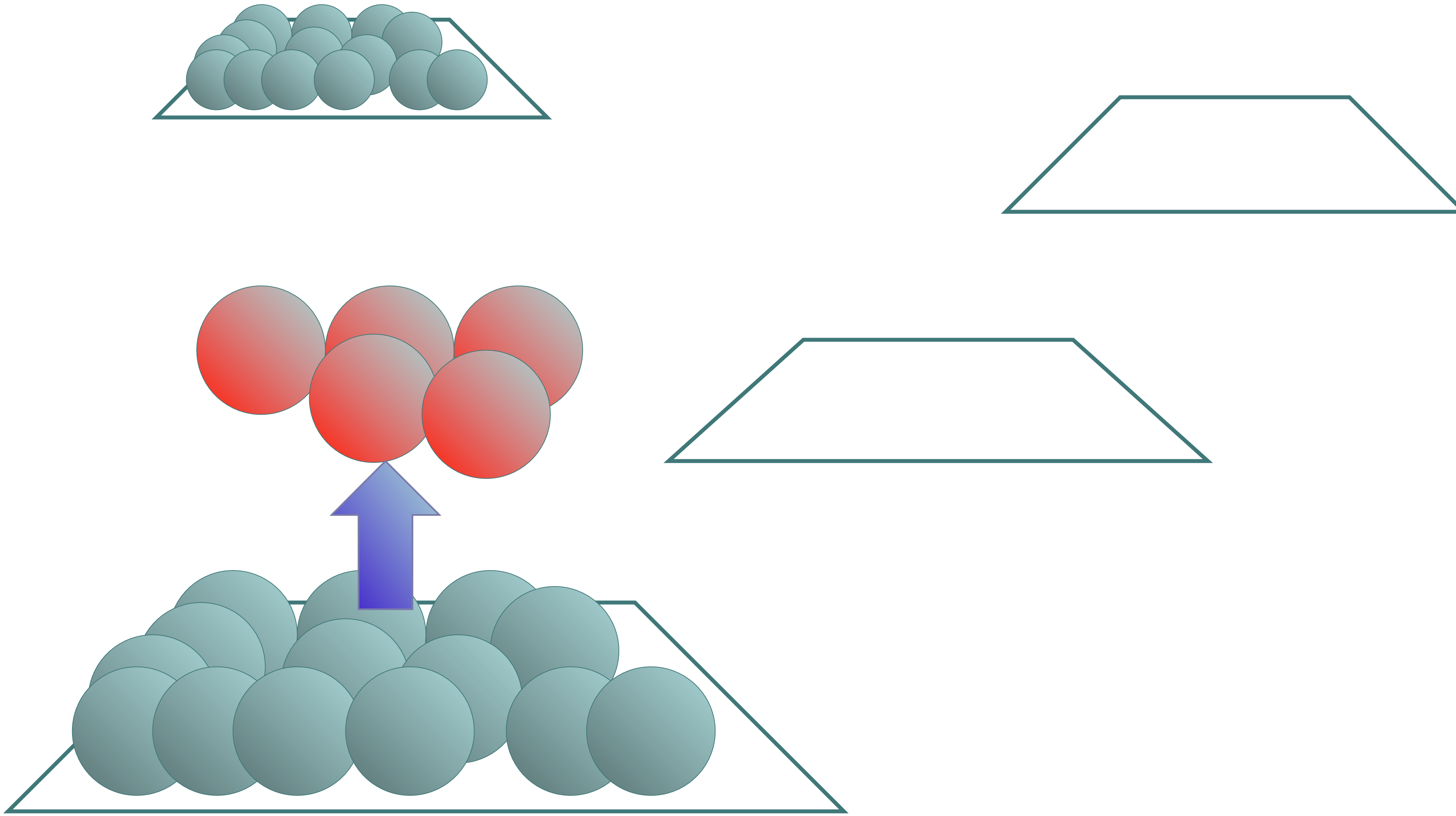
$$\frac{\mathrm{d}p}{\mathrm{d}t} = \overbrace{cp(h-p)}^{} - \overbrace{ep}^{}$$

Evolution of dispersal

Predator-prey metacommunity dynamics



Predator-prey metacommunity dynamics



Evolution of dispersal

Metacommunity dynamics

Predator-prey metacommunity

$$\frac{dR}{dt} = c_R R(h - R) - e_R R - \boxed{\mu} P \qquad \text{(prey)}$$

$$\frac{dP}{dt} = c_P P(R - P) - e_P P - (e_R + \boxed{\mu})P \qquad \text{(predator)}$$

Model framework and assumptions

- Model based on Jansen and Vitalis (2007)
- Increased dispersal **between** patches comes at cost of decreasing **local** fitness
- Need to have a link between **local** within-patch dynamics (i.e., fitness) and regional **metacommunity**-level processes (colonization-extinction)

Evolution of dispersal

Model framework and assumptions

Regional metacommunity scale

$$\frac{dR}{dt} = c_R R(h - R) - e_R R - \mu P \qquad \text{(prey)}$$

$$\frac{dP}{dt} = c_P P(R - P) - e_P P - (e_R + \mu)P \qquad \text{(predator)}$$

Local within-patch scale

$$\dot{x} = rx\left(1 - \frac{x}{K}\right) - \gamma_x x - axy \qquad \text{(prey equation)}$$

$$\dot{y} = aqxy - \gamma_y y - my \qquad \text{(predator equation)}$$

Evolution of dispersal

Local (within-patch) dynamics

$$\dot{x} = rx\left(1 - \frac{x}{K}\right) - \gamma_x x - axy \qquad \text{(prey equation)}$$

$$\dot{y} = aqxy - \gamma_y y - my \qquad \text{(predator equation)}$$

Evolution of dispersal

Local (within-patch) dynamics

$$\dot{x} = rx\left(1 - \frac{x}{K}\right) - \boxed{\gamma_x}x - axy \qquad \text{(prey equation)}$$

$$\dot{y} = aqxy - \boxed{\gamma_y}y - my \qquad \text{(predator equation)}$$

$$\Downarrow$$

$$\tilde{x}_0 = \frac{K}{r}(r - \boxed{\gamma_x}) \qquad \text{(local prey density without predator)}$$

$$\tilde{x}_P = \frac{(m + \gamma_y)}{aq}, \qquad \text{(local prey density with predator)}$$

$$\tilde{y} = \frac{r}{a}\left(1 - \frac{m + \boxed{\gamma_y}}{aqK}\right) - \frac{\gamma_x}{a}, \qquad \text{(local predator density)}$$

Evolution of dispersal

Model framework and assumptions

Regional metacommunity scale

$$\frac{dR}{dt} = c_R R(h - R) - e_R R - \mu P \qquad \text{(prey)}$$

$$\frac{dP}{dt} = c_P P(R - P) - e_P P - (e_R + \mu)P \qquad \text{(predator)}$$

$$\Downarrow$$

When metacommunity is at equilibrium

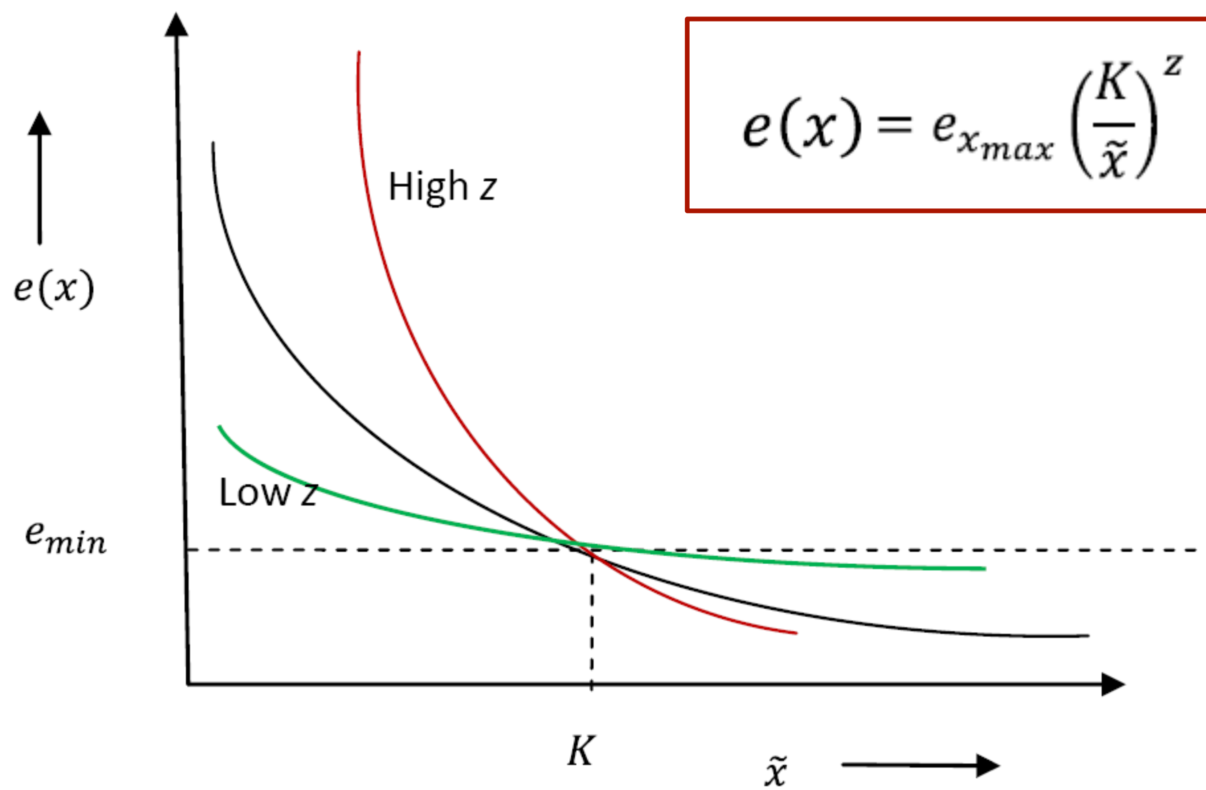
$$\tilde{R} = \frac{1}{2}\left[1 - \left(\frac{e_R + \mu}{c_{R_P}}\right) + \Gamma\right] + \frac{1}{2}\sqrt{\left[1 - \left(\frac{e_R + \mu}{c_{R_P}}\right) + \Gamma\right]^2 + 4\left(\frac{\mu - \Delta c_R}{c_{R_P} c_P}\right)(e_P + e_R + \mu)},$$

$$\tilde{P} = \tilde{R} - \frac{(e_P + e_R + \mu)}{c_P}$$

Evolution of dispersal

Scaling up from local (within-patch) dynamics to regional metacommunity dynamics

Frequency of local prey subpopulation extinction, e



$$e(x) = e_{x_{max}} \left(\frac{K}{\tilde{x}}\right)^z$$

Local prey density, x

Evolution of dispersal
Measuring fitness in a metacommunity

- Utilize this framework to study evolution of dispersal, γ, in a metacommunity.

Evolution of dispersal
Measuring fitness in a metacommunity

- Follow the fate of a single single mutant invasive individual, with dispersal strategy γ_{mutant}, invading a metacommunity with a resident prey with dispersal rate, $\gamma_{resident}$, while both resident predator, *P*, and prey, *R*, patch-occupancies are at equilibrium.

Evolution of dispersal

Measuring fitness in a metacommunity

- Measure the total lifetime reproductive output of the focal invasive after it has landed in a patch, before going extinct, or being competitively displaced.
- Use R_M as a measure of fitness (Metz and Gyllenberg, 2001; similar to R_0).

Evolution of dispersal

Measuring fitness in a metacommunity

Fitness of single mutant invasive prey

$W =$

Evolution of dispersal

Measuring fitness in a metacommunity

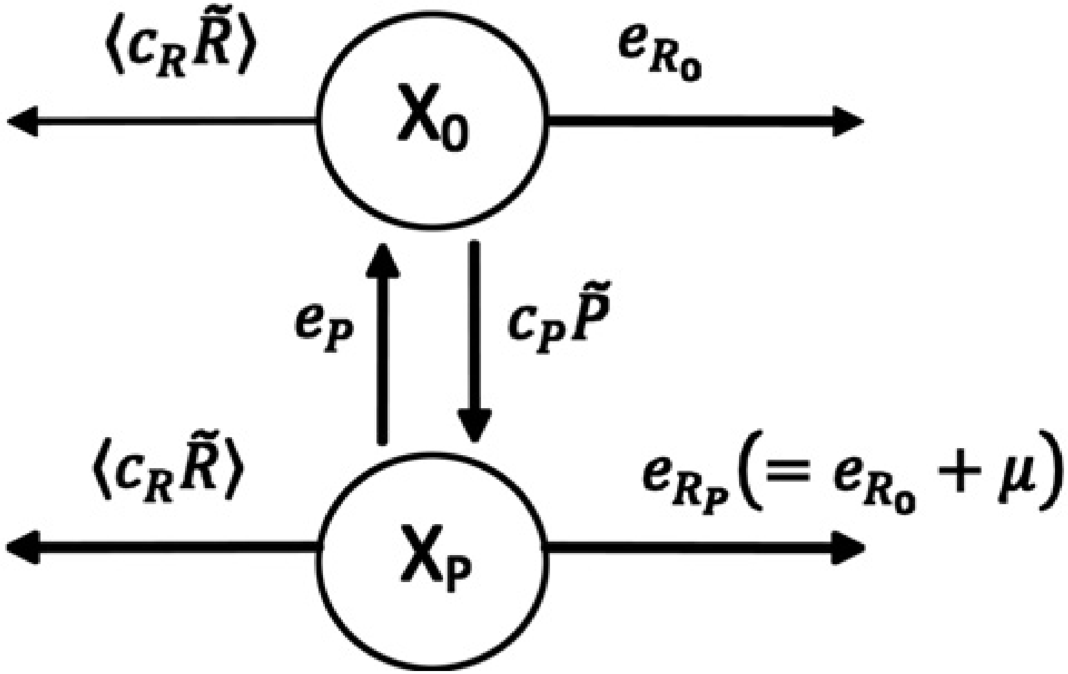
Fitness of single mutant invasive prey

$$W = \left(\text{prob. mutant landing on empty patch} \right) \times \left(\text{Number of colonizers produced before extinction or complete competitive displacement} \right)$$

Evolution of dispersal

Measuring fitness in a metacommunity

State transition diagram for an invasive prey patch prior to extinction or reinvasion by a resident



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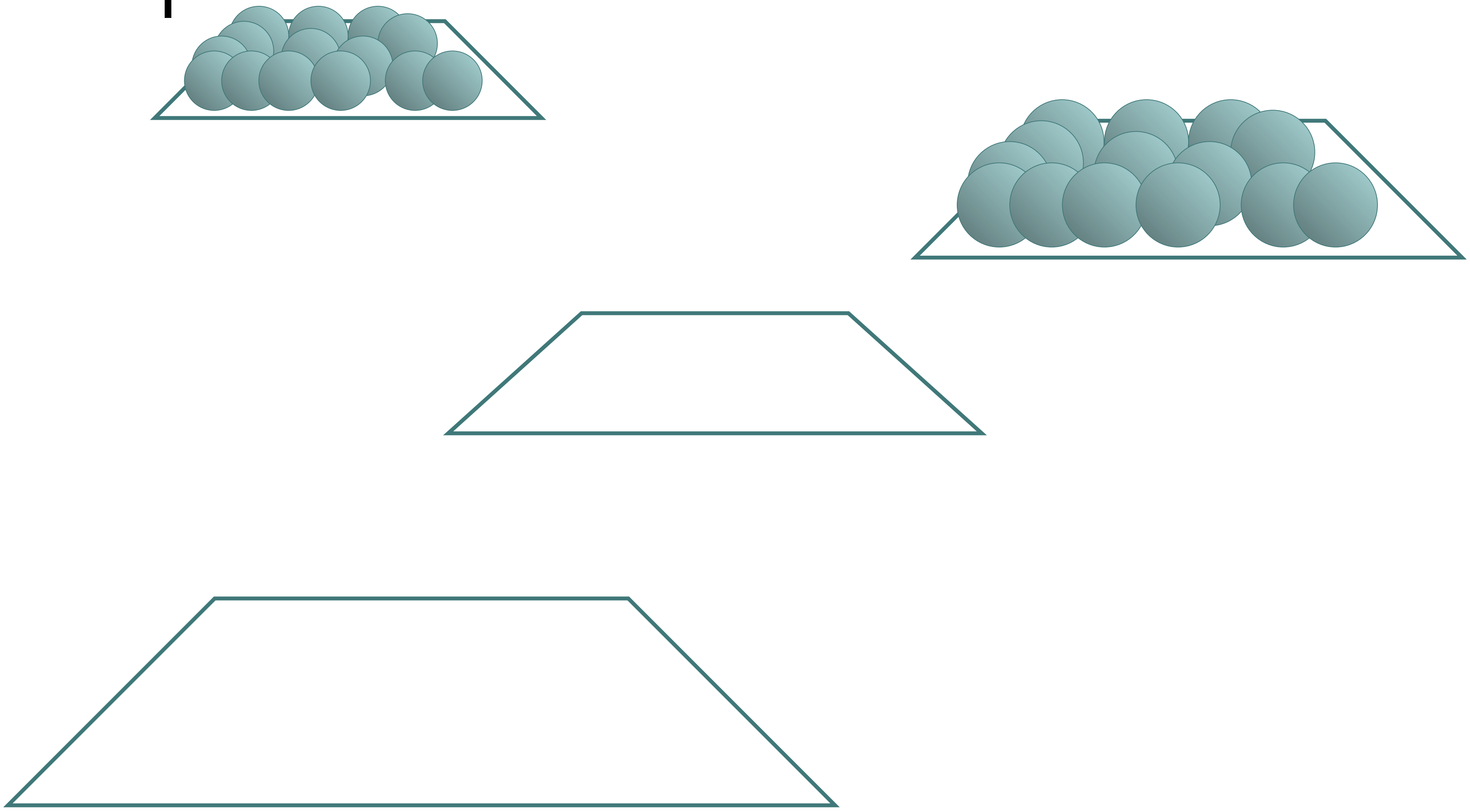

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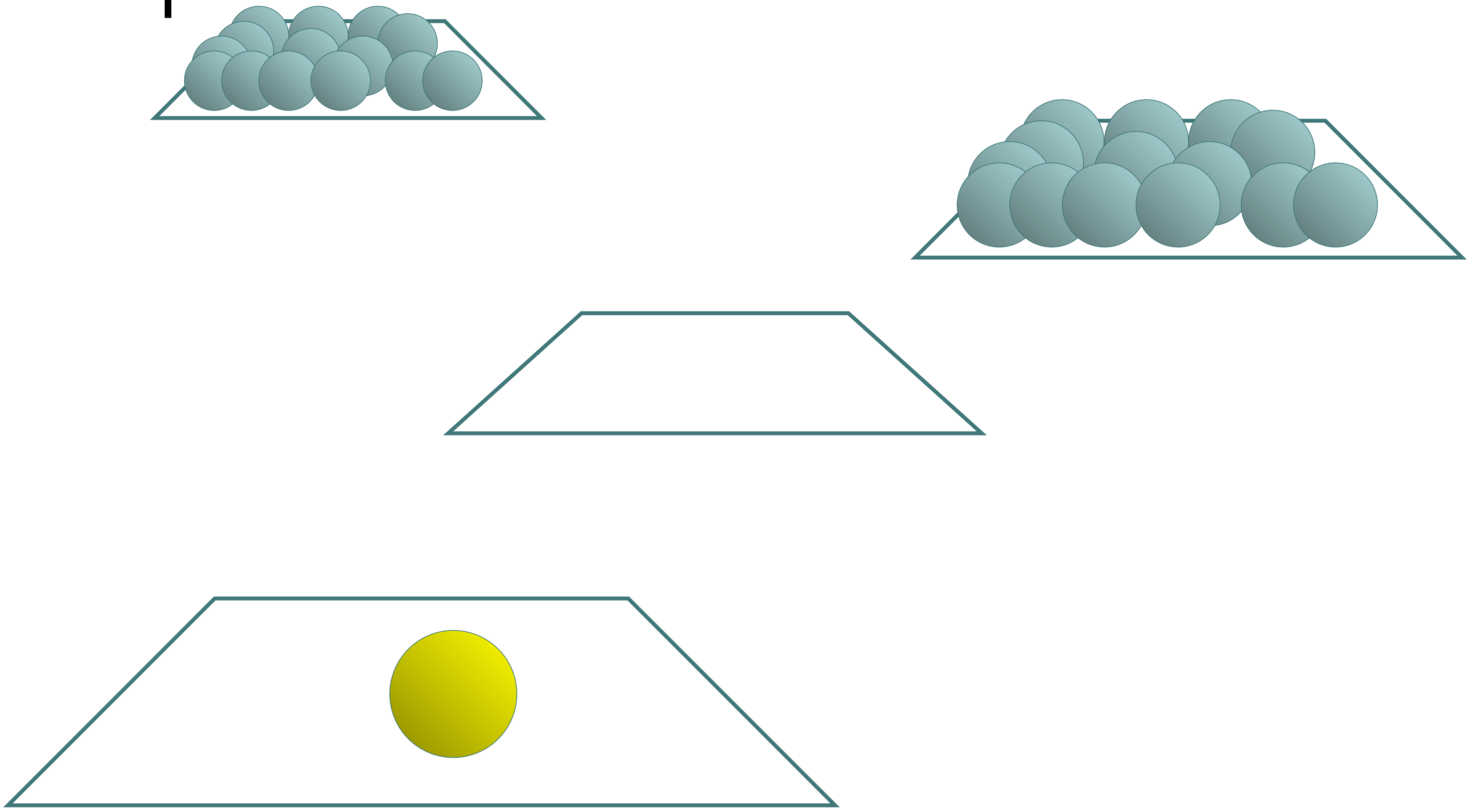

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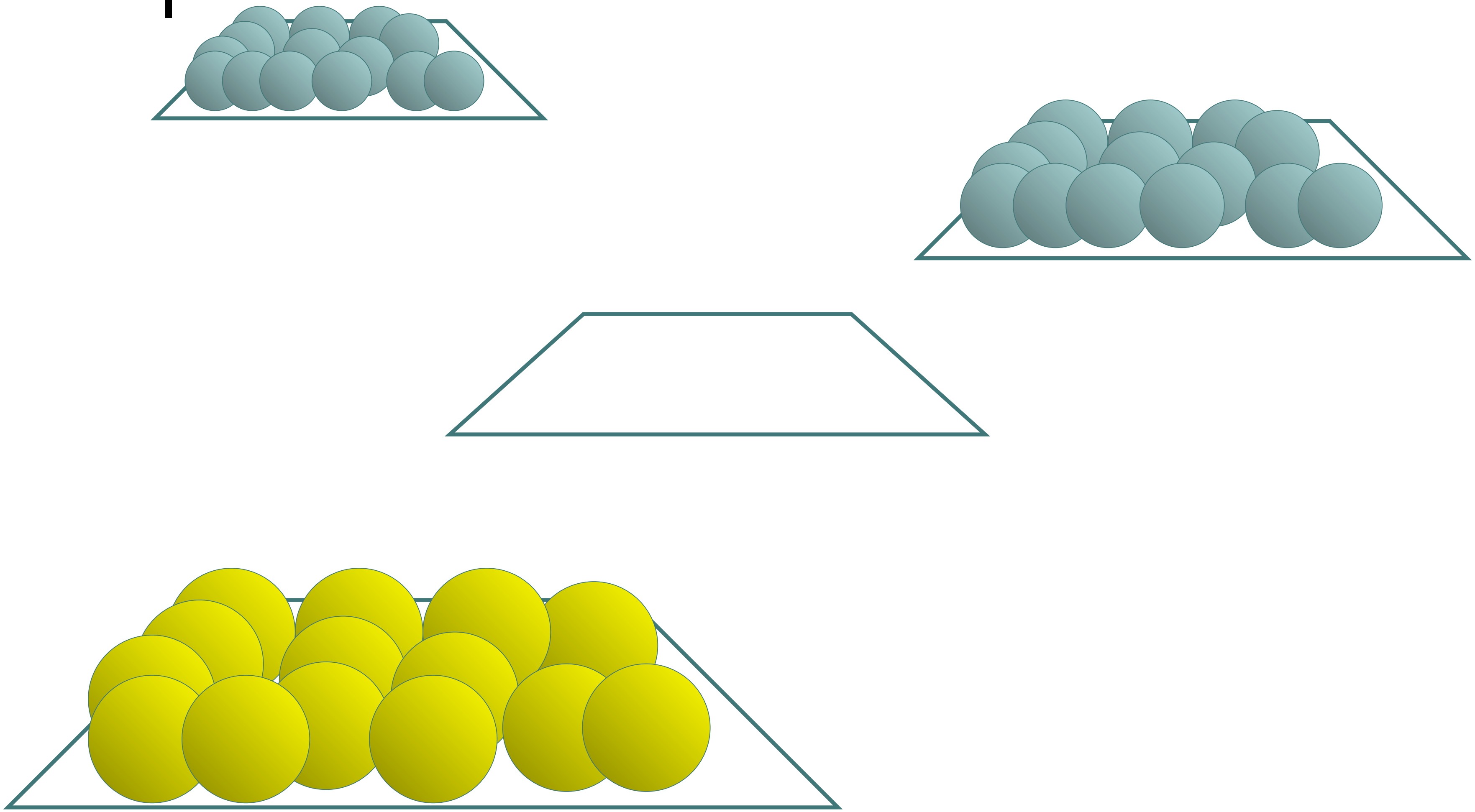

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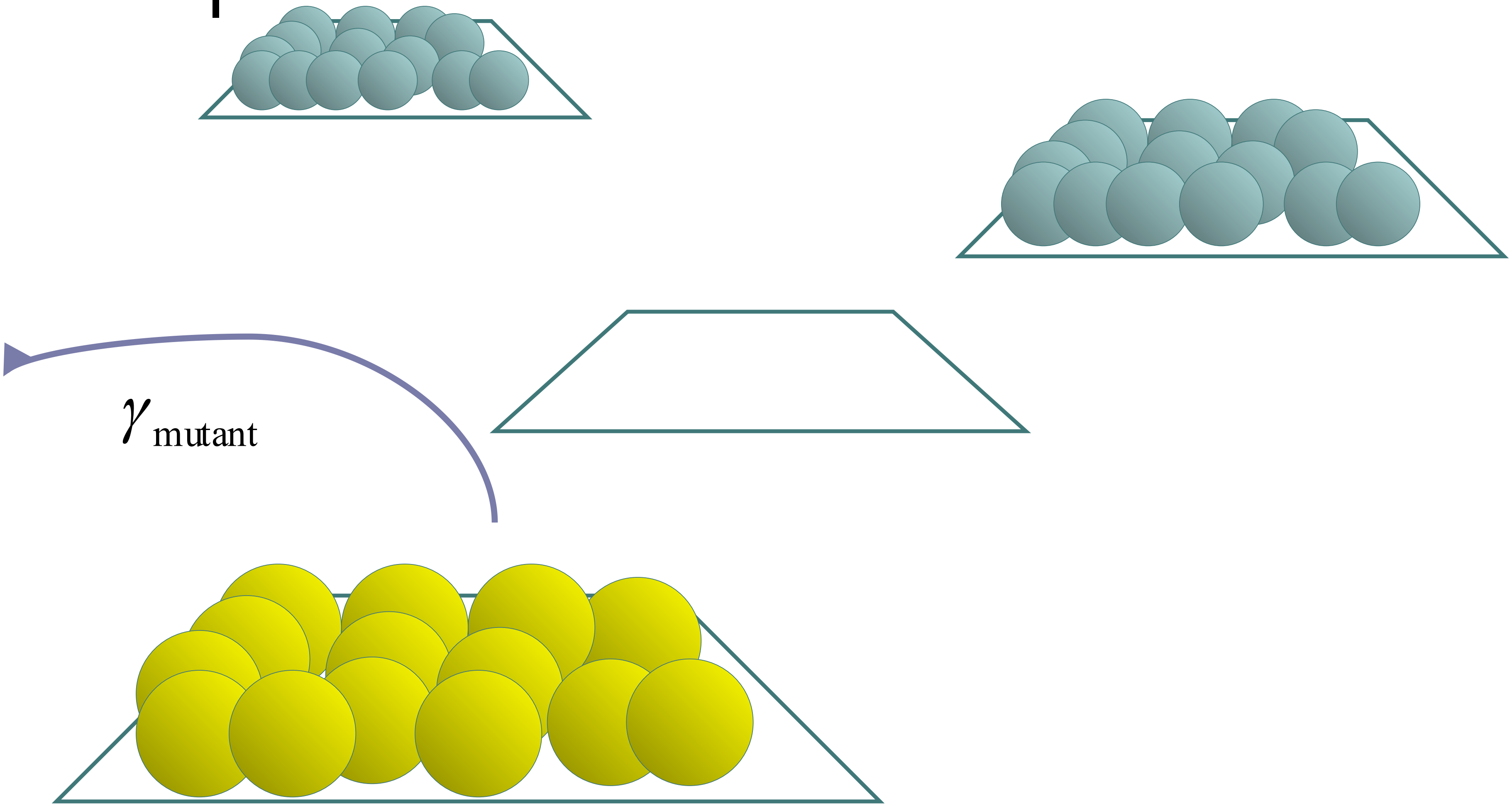

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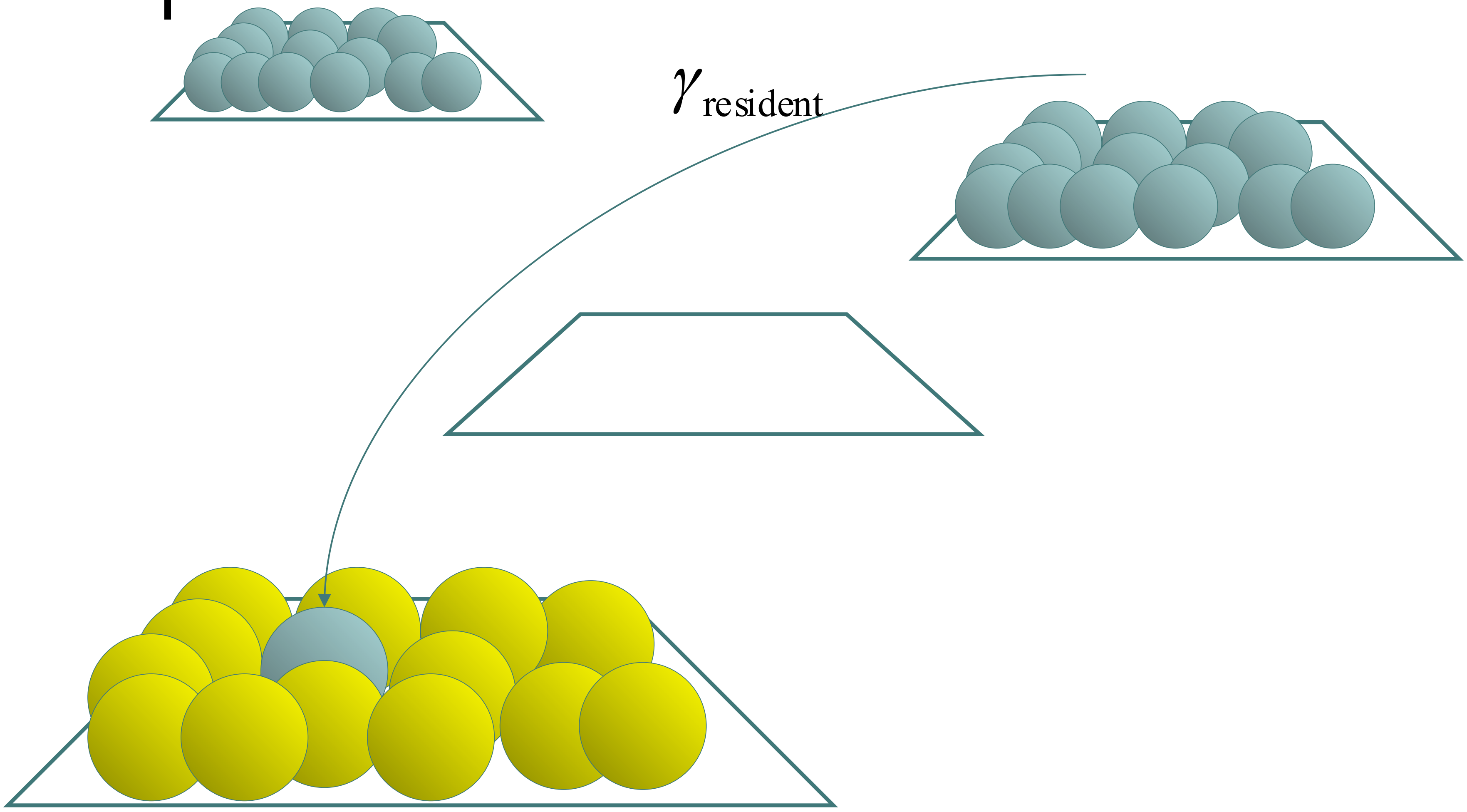

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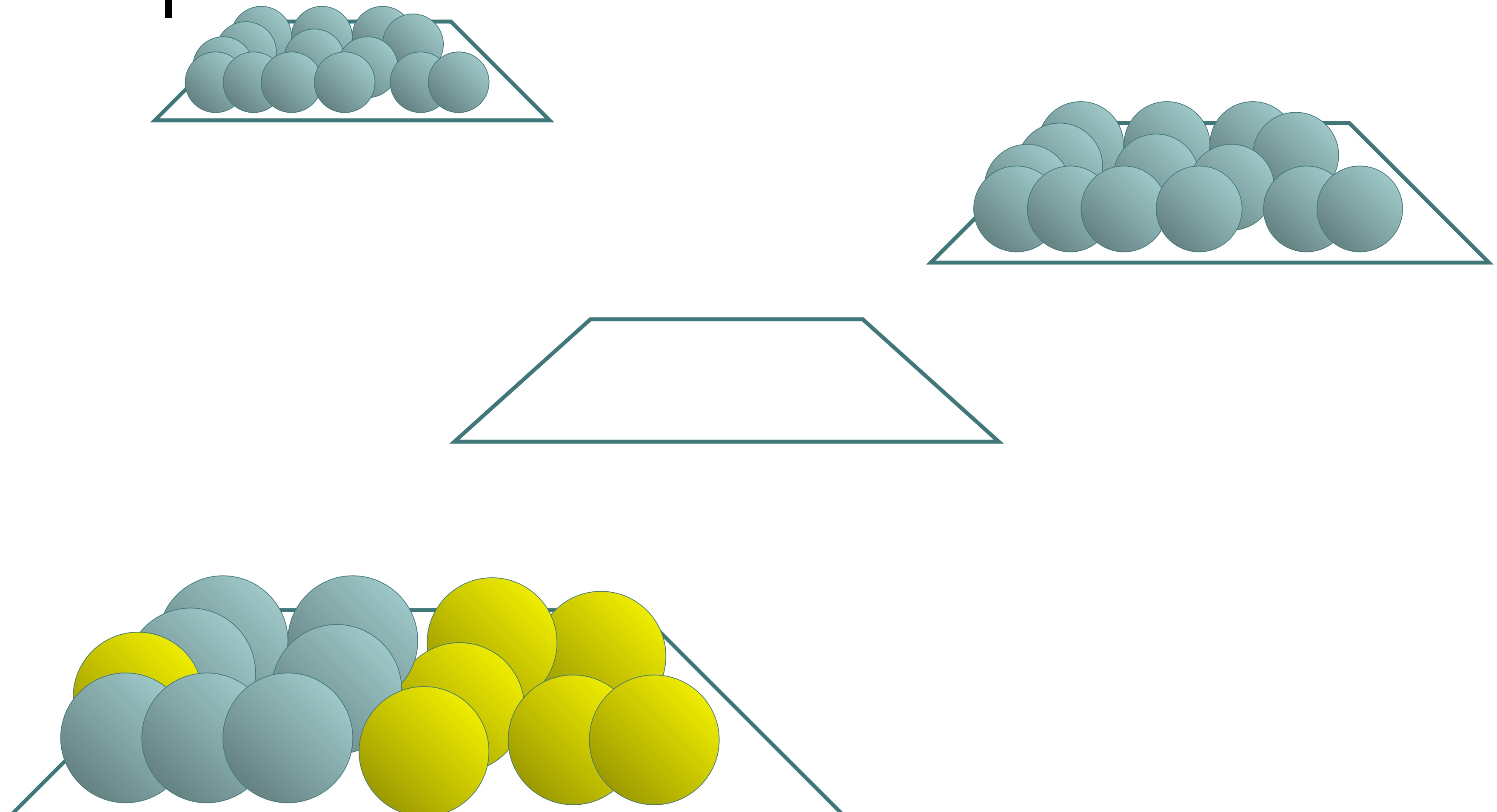

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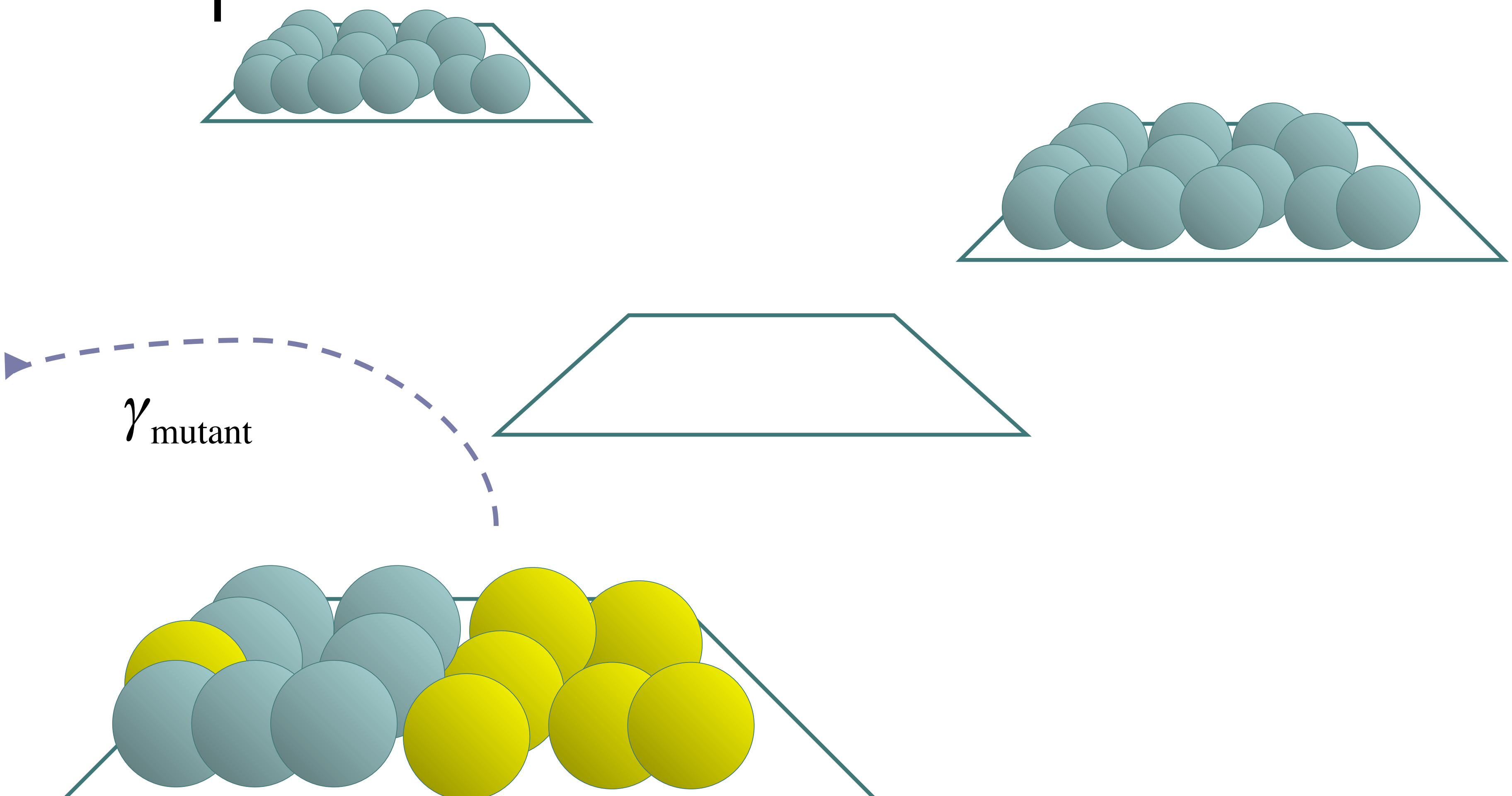

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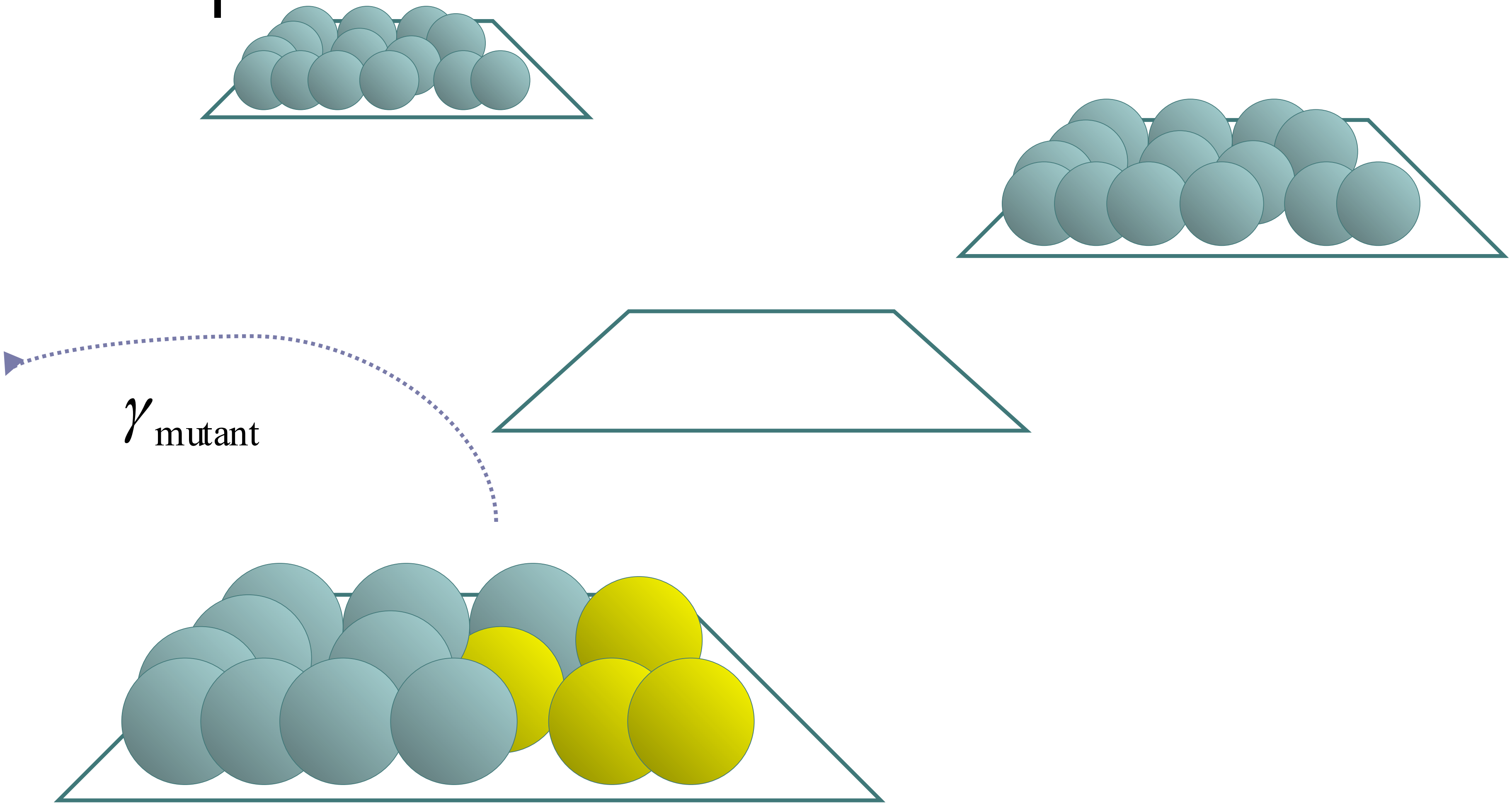

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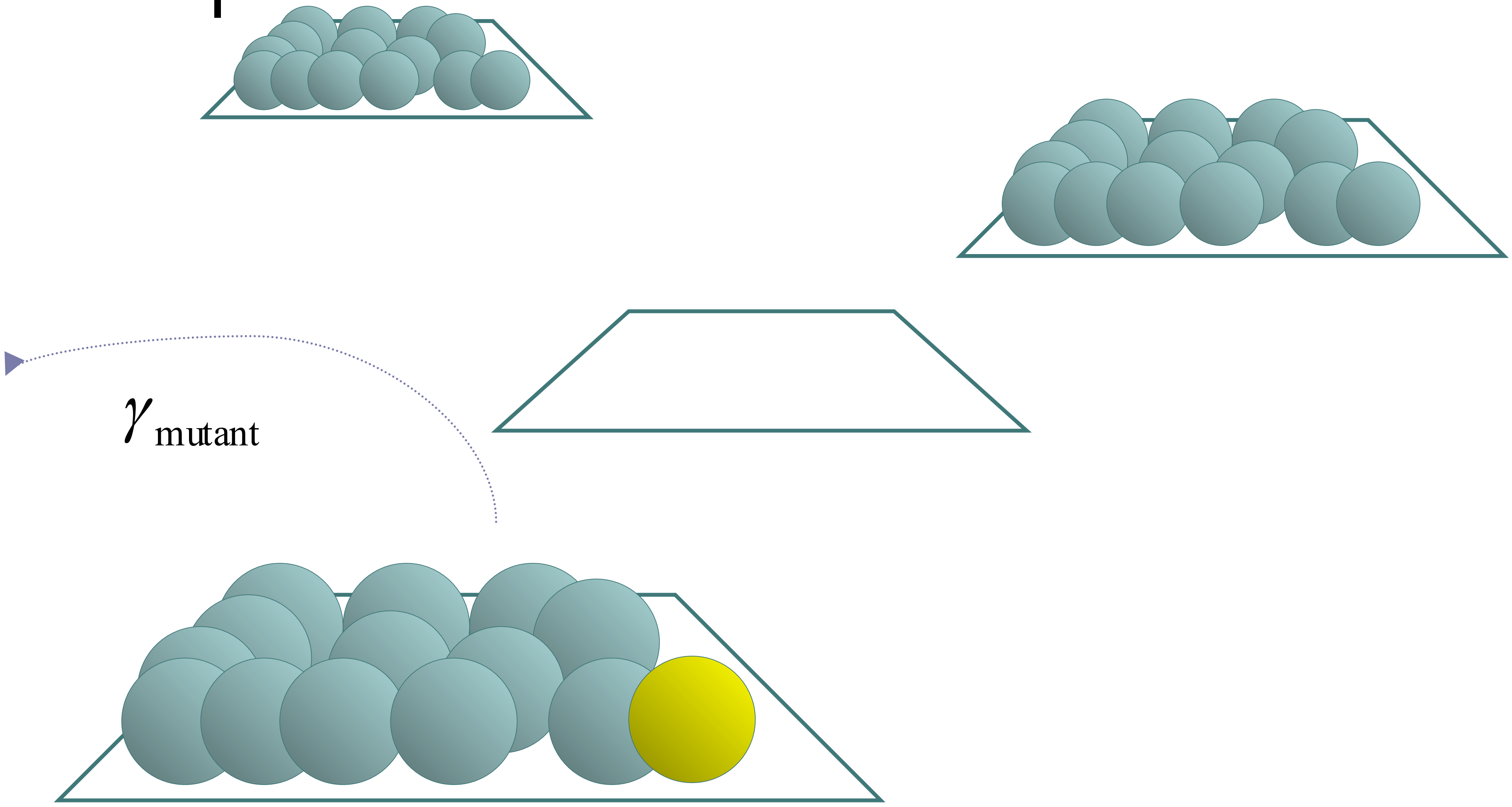

Evolution of dispersal

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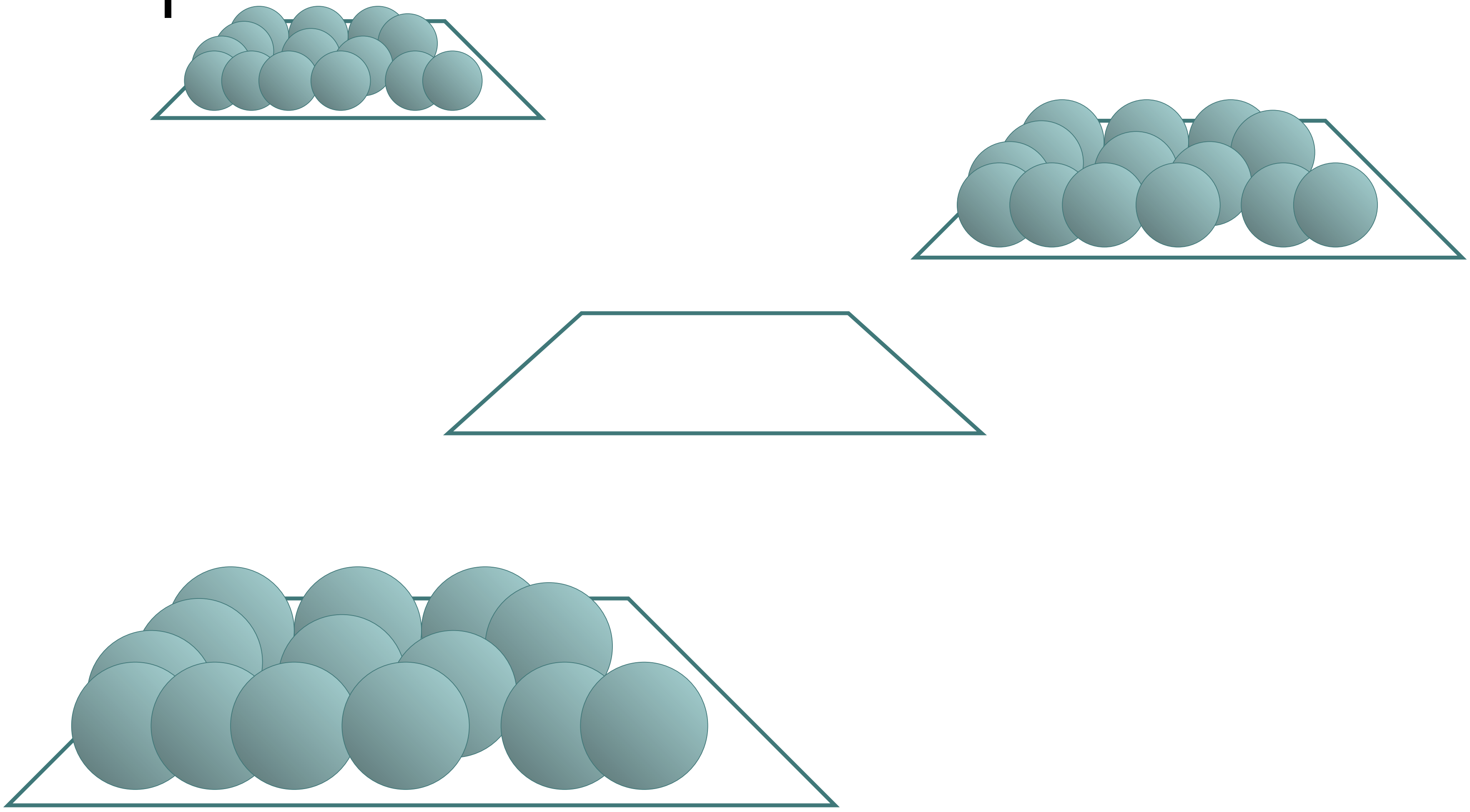


Evolution of dispersal

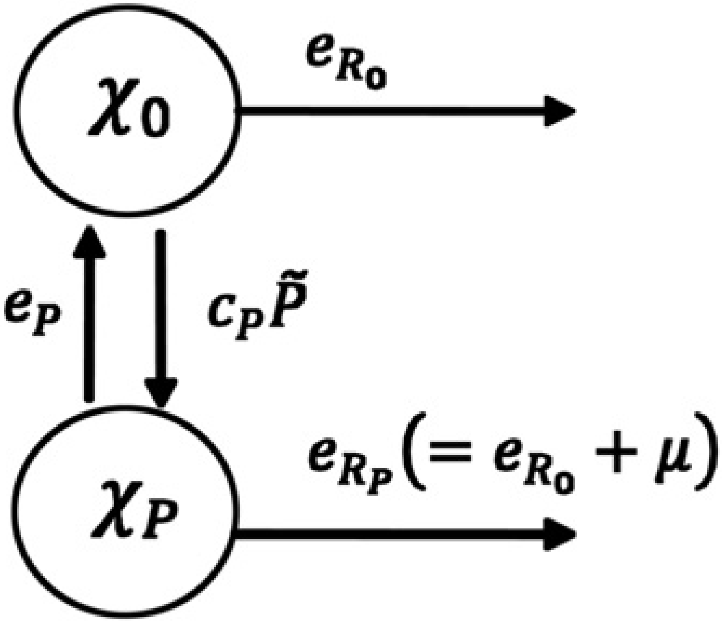
Measuring fitness in a metacommunity

- Involves measuring the output of a mixed strategy patch (when both resident and invasive strategy are present).

Evolution of dispersal

Measuring fitness in a metacommunity

State transition diagram for an mixed-strategy prey patch prior to extinction



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Evolution of dispersal

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$$W = \left(\text{prob. mutant landing on empty patch} \right) \times \left(\text{Number of colonizers produced before extinction or complete competitive displacement} \right)$$

Measuring fitness in a metacommunity

Fitness of single mutant invasive prey

$$W = \left(\text{prob. mutant landing on empty patch}\right) \times \left(\text{Number of colonizers produced before extinction or complete competitive displacement}\right) + \left(\text{prob. invasive landing on resident prey-only patch}\right) \times \left(\text{Number of colonizers produced before extinction or complete competitive displacement}\right)$$

Measuring fitness in a metacommunity

Fitness of single mutant invasive prey

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$$+ \left(\text{prob. invasive landing on resident predator-prey patch}\right) \times \left(\text{Number of colonizers produced before extinction or complete competitive displacement}\right)$$

Evolution of dispersal

Gradient of selection and evolutionarily singular strategy

$$G = \left.\frac{\partial W}{\partial \gamma_{\mathrm{m}}}\right|_{\gamma_{\mathrm{mutant}}=\gamma_{\mathrm{resident}}} = 0$$

Evolutionary singular strategy: γ^{*} (Critical value of dispersal)

Evolution of dispersal

Condition ESS and CSS

If $\left.\frac{dG}{d\gamma}\right|_{\gamma=\gamma^*} < 0$ $\quad\gamma^*$ is an evolutionary attractor

If $\left.\frac{\partial^2 W}{\partial \gamma_m^2}\right|_{\gamma_{\mathrm{mutant}}=\gamma_{\mathrm{resident}}} < 0$ $\quad\gamma^*$ is **ESS stable**

(**not** a potential evolutionary branching point)

If both of the above, then **Continuously Stable Strategy**

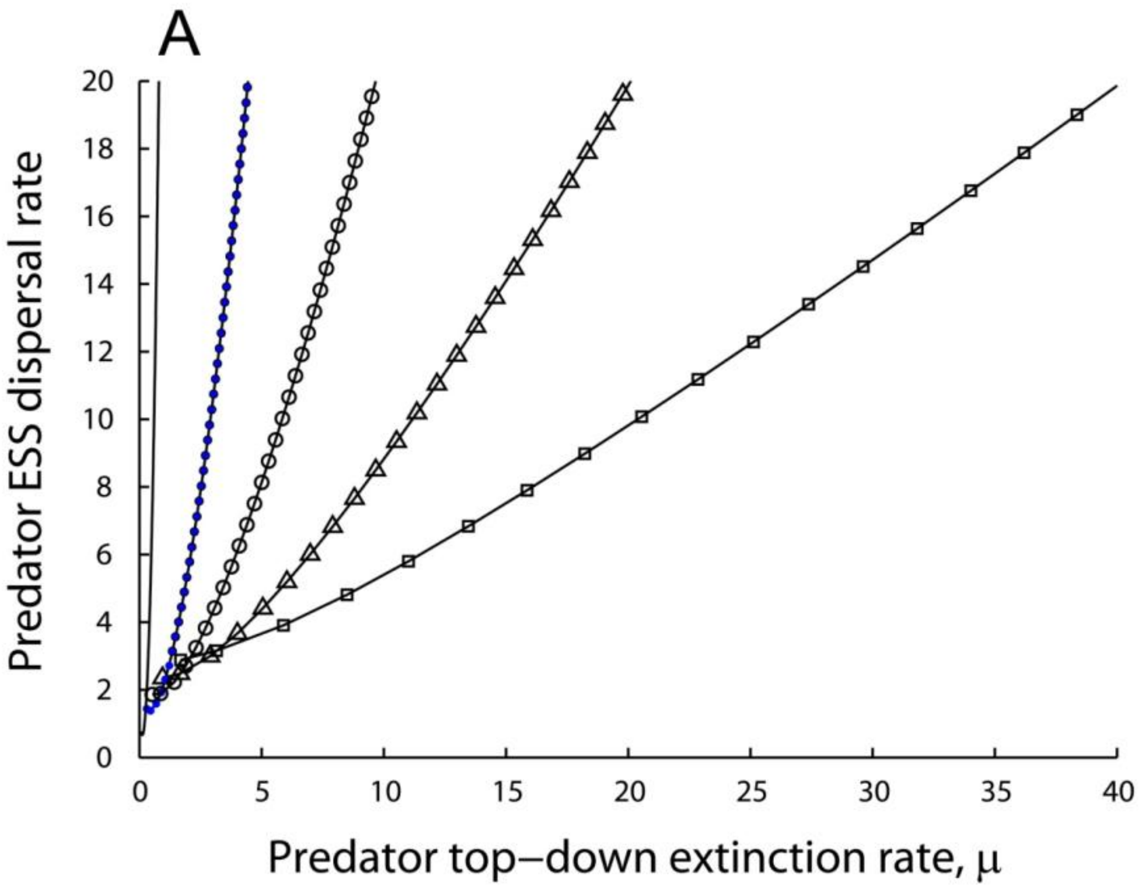
Evolution of dispersal

Research Question

- Want to measure how evolutionary stable (ESS) dispersal will change with increasing extinction rates caused by unstable interaction with predator

Evolution of dispersal

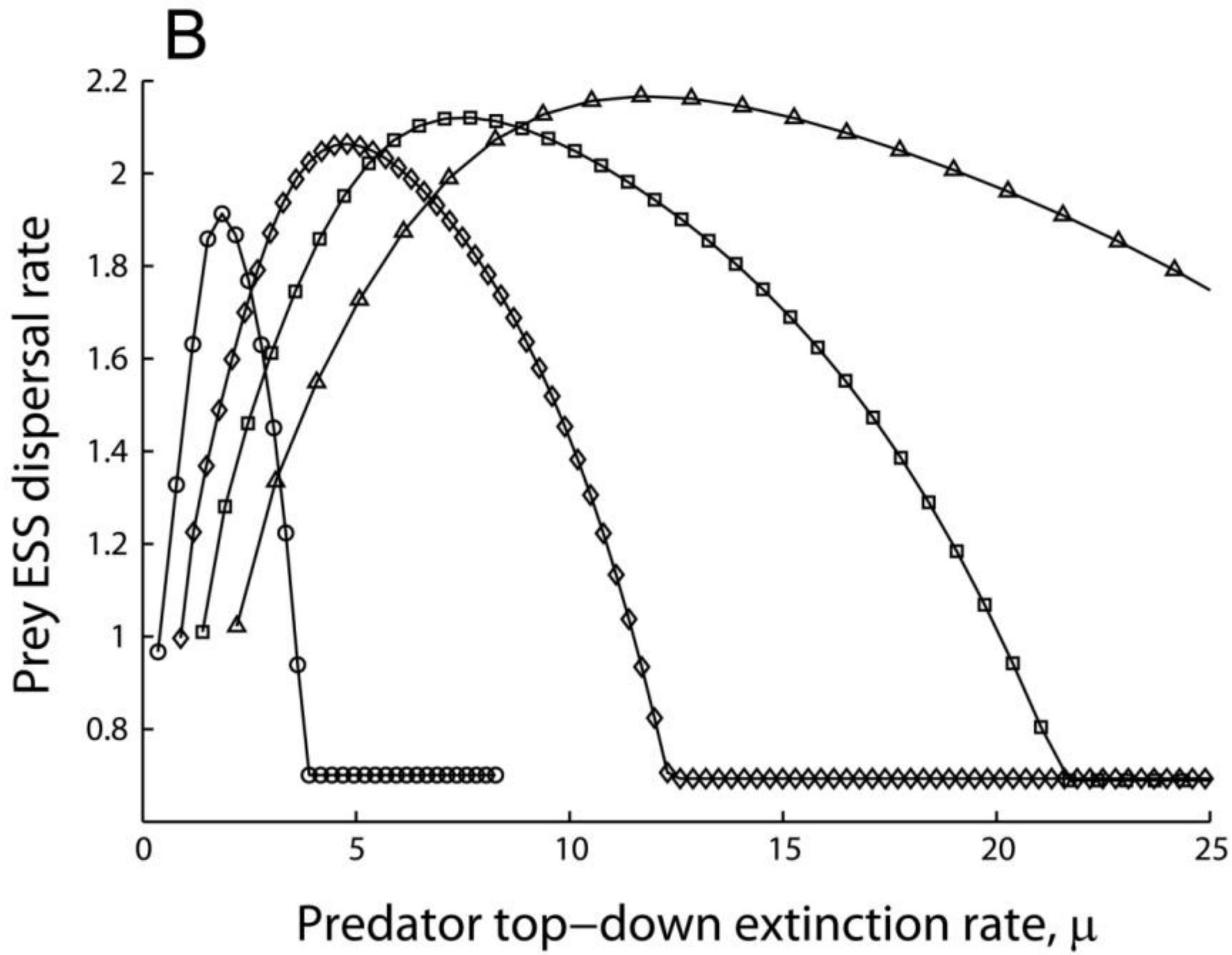
Results: <u>predator</u> ESS dispersal with increasing top-down extinction



Pillai, Gonzalez and Loreau American Naturalist, 2012

Evolution of dispersal

Results: prey ESS dispersal with increasing top-down extinction



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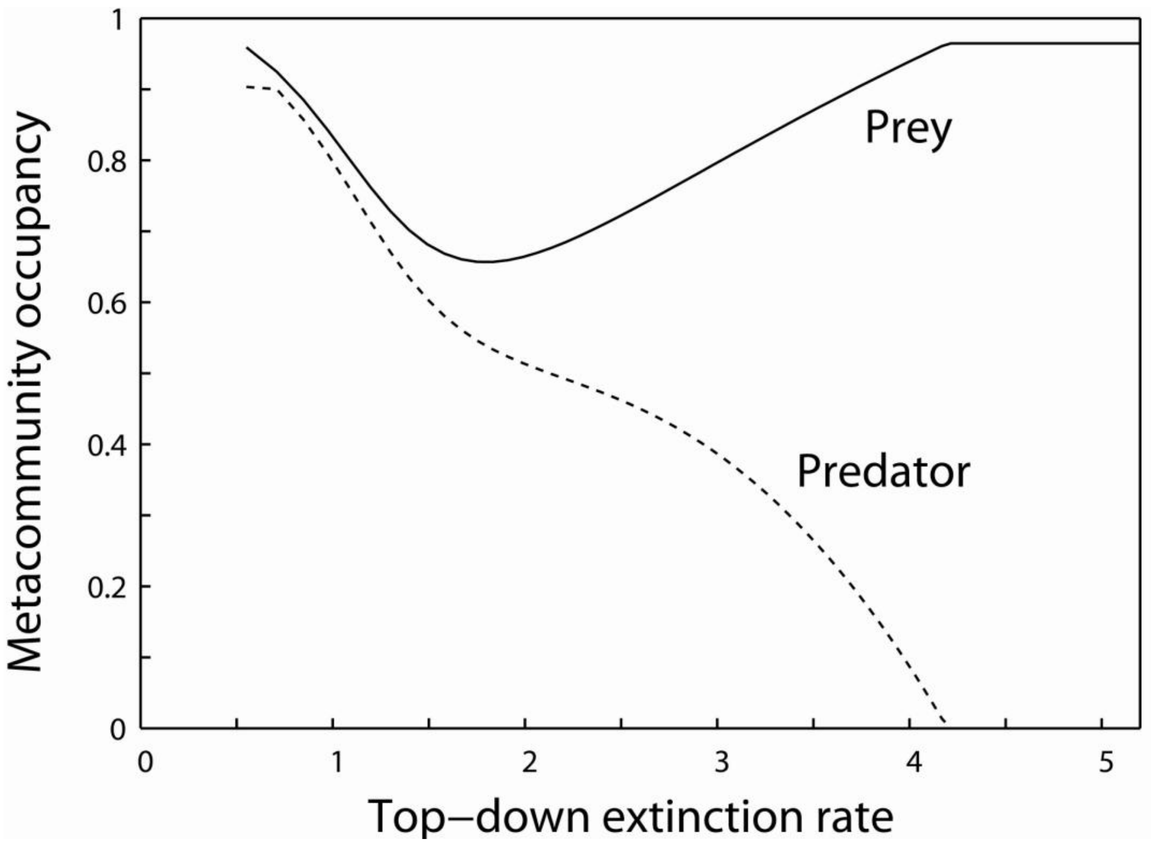
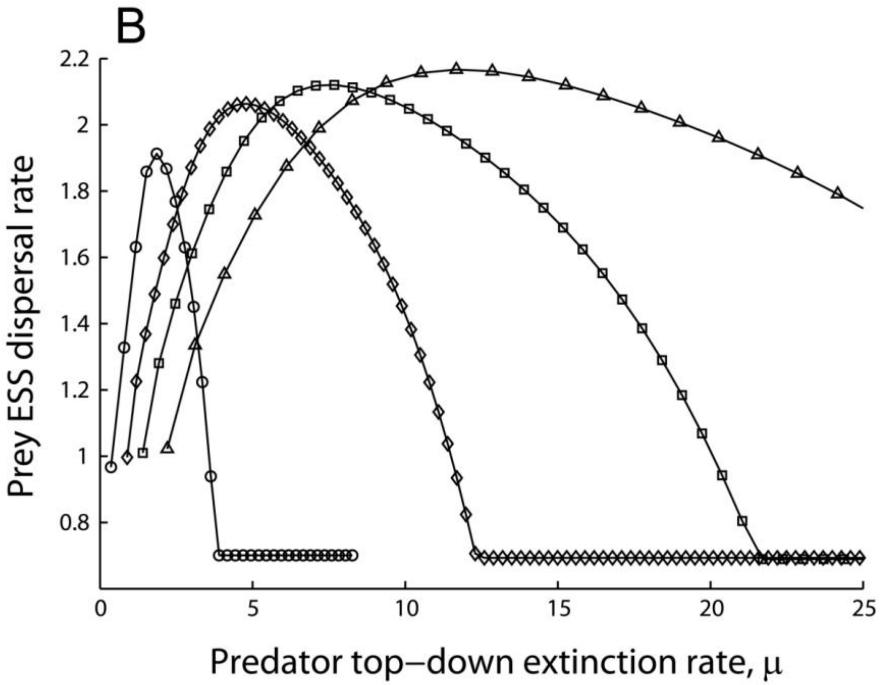
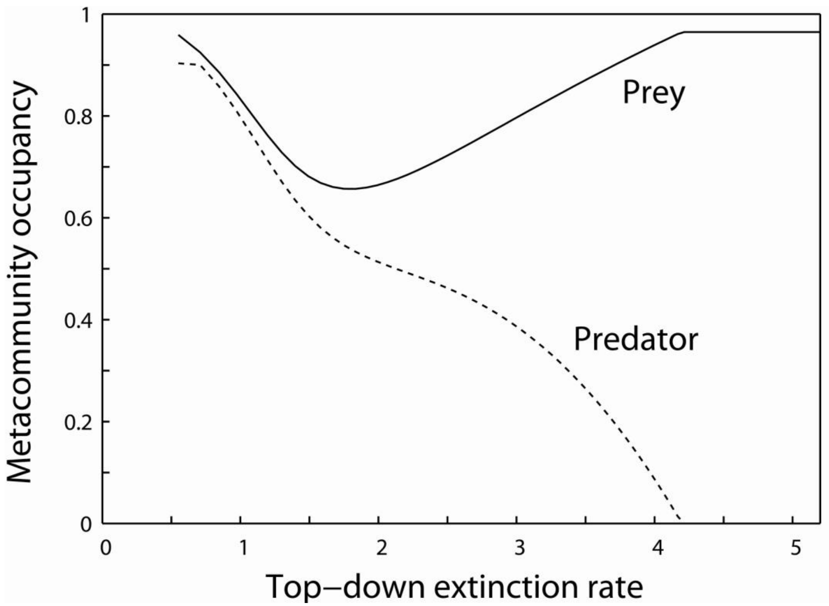
Evolution of dispersal

Results: <u>prey</u> ESS dispersal with increasing top-down extinction



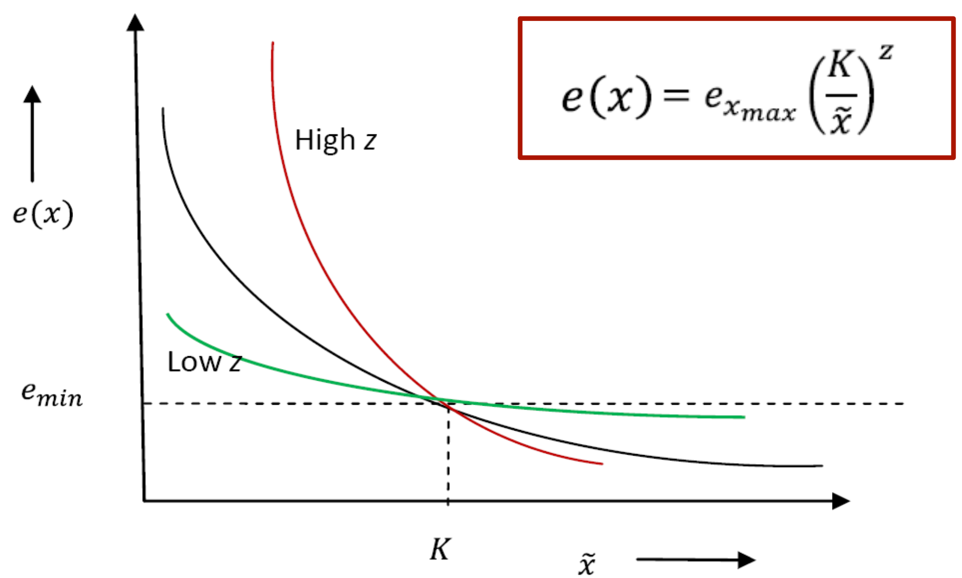
Evolution of dispersal
Results: prey ESS dispersal with increasing top-down extinction





Evolution of dispersal

Results: prey ESS dispersal with increasing top-down extinction



Frequency of local prey subpopulation extinction, e

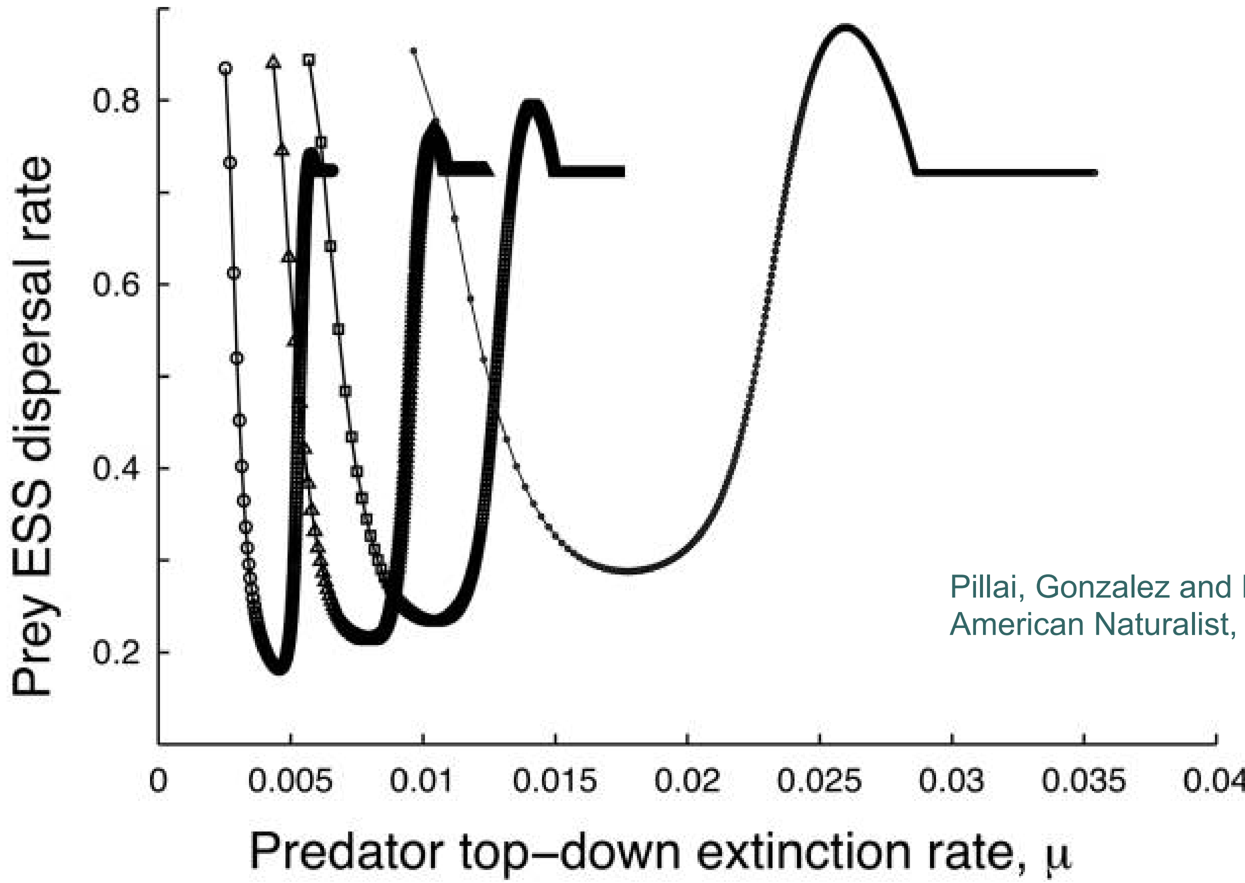
Local prey density, x

Evolution of dispersal

Results: <u>prey</u> ESS dispersal with increasing top-down extinction

For very low z_x values.

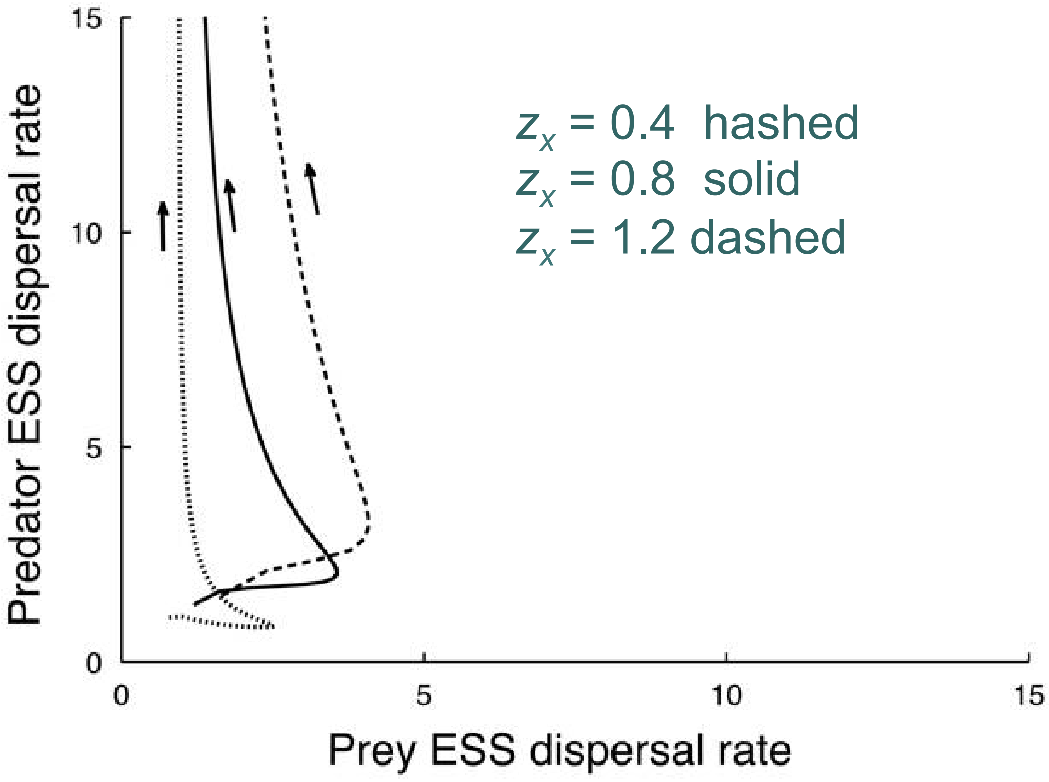
Curves shown for
z_x =0.01 (circles)
z_x =0.08 (triangles)
z_x =0.10 (squares)
z_x =0.15 (dots)



Pillai, Gonzalez and Loreau, American Naturalist, 2012

Evolution of dispersal
Results: Coevolution of a predator and prey

Joint evolutionary stable strategy for coevolved predator and prey



z_x = 0.4 hashed
z_x = 0.8 solid
z_x = 1.2 dashed

Pillai, Gonzalez and Loreau, American Naturalist, 2012

Summary of results

- Extinctions are caused by interspecific (trophic) interactions
- Feedback between local and metacommunity scale processes: predator-prey interactions play out differently at local and regional scales

Conclusions and Summary

- Some patterns and processes are emergent at the metacommunity scale
- Non-monotonic dispersal is an **emergent property** at the scale of the metacommunity arising from contradiction between local and metacommunity scale selection processes

Acknowledgements

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