A theoretical framework for trait-based eco-evolutionary dynamics: population structure, intraspecific variation, and community assembly

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Trait variation across levels of organization

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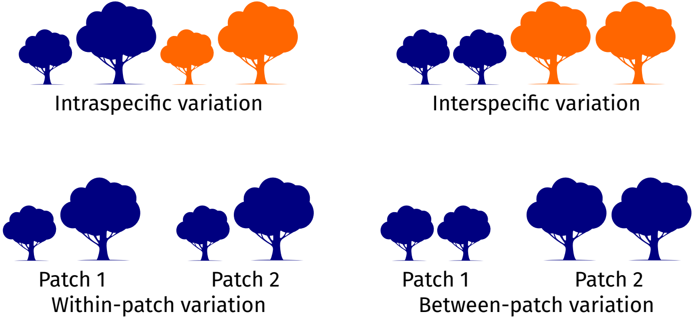

Image: wikimedia

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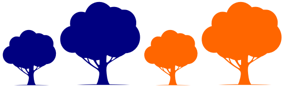
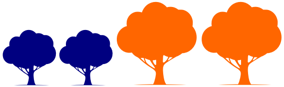
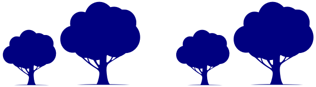


Intraspecific variation



Interspecific variation



Patch 1 Patch 2

Within-patch variation

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Between-patch variation

- How does ITV affect higher-level outcomes like species coexistence and ecosystem functioning? (Bolnick et al., 2011; Violle et al., 2012; Raffard et al., 2019)

Image: wikimedia

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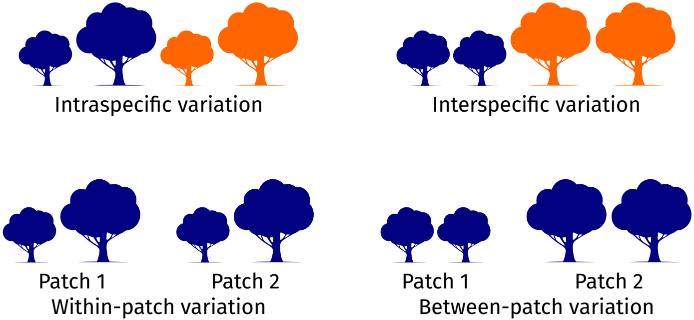


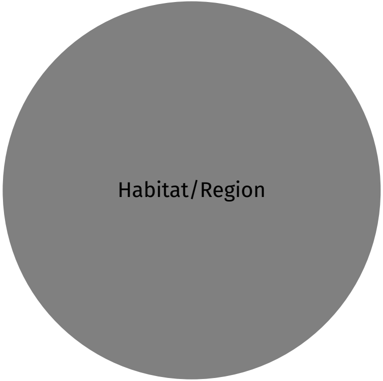
- How does ITV affect higher-level outcomes like species coexistence and ecosystem functioning? (Bolnick et al., 2011; Violle et al., 2012; Raffard et al., 2019)
- How necessary is it to include ITV to understand your study system/answer your questions?

Image: wikimedia

Eco-evolutionary dynamics and evolutionarily stable communities (ESCs)

- Heritable trait variation that affects fitness
  $\Longrightarrow$ eco-evolutionary dynamics

Geritz et al. (1998), Edwards et al. (2018), Klausmeier et al. (2020)



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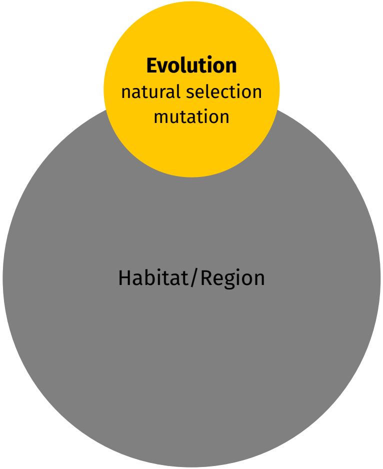

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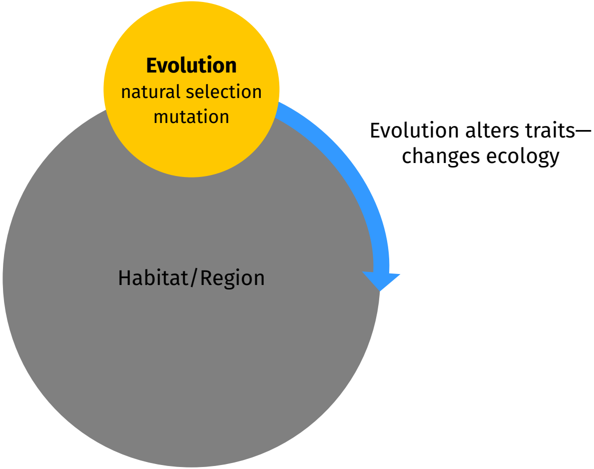

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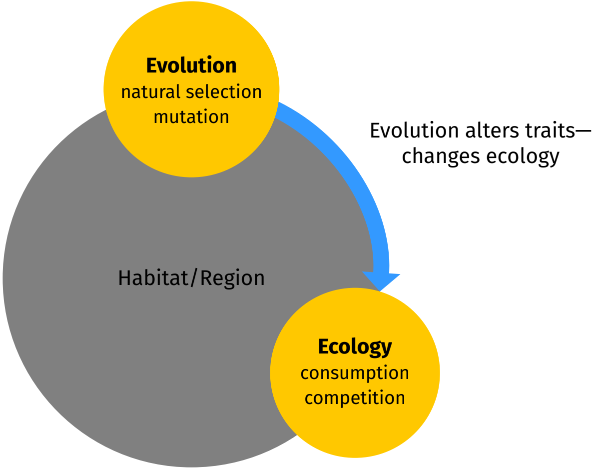

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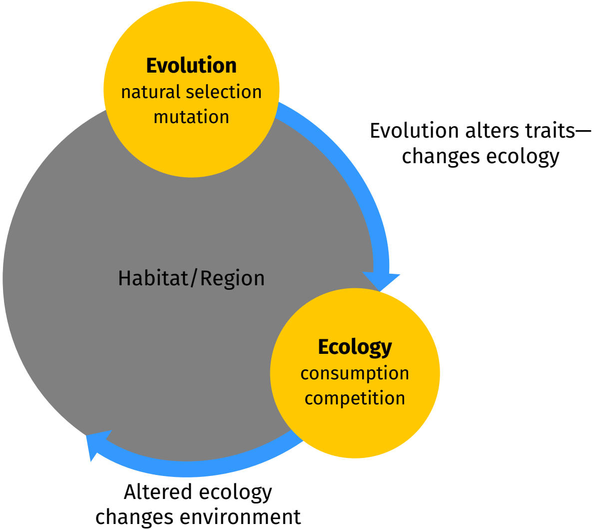

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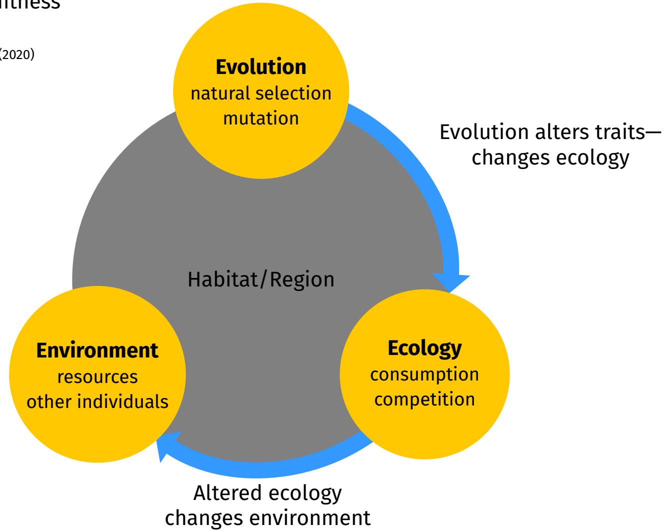

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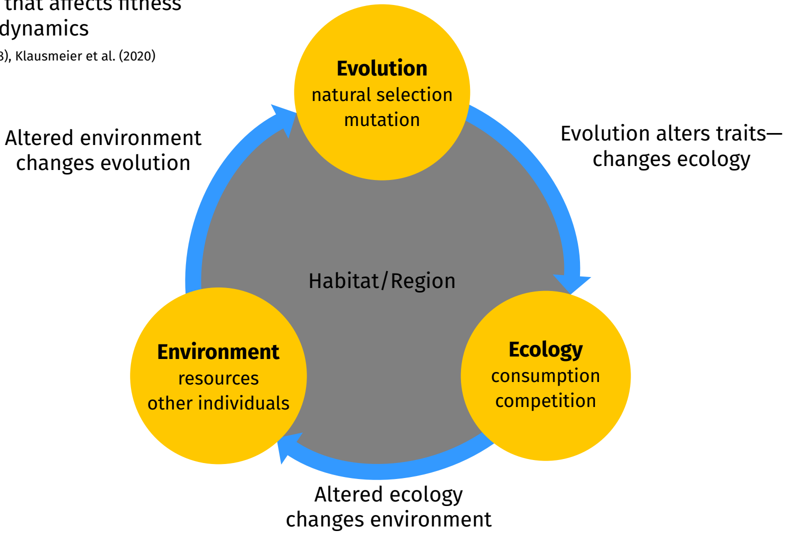

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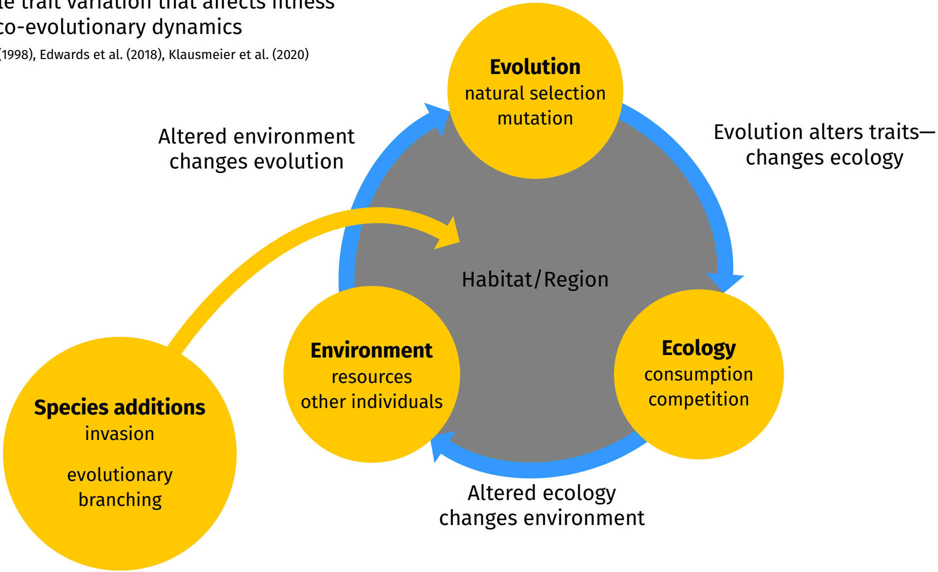

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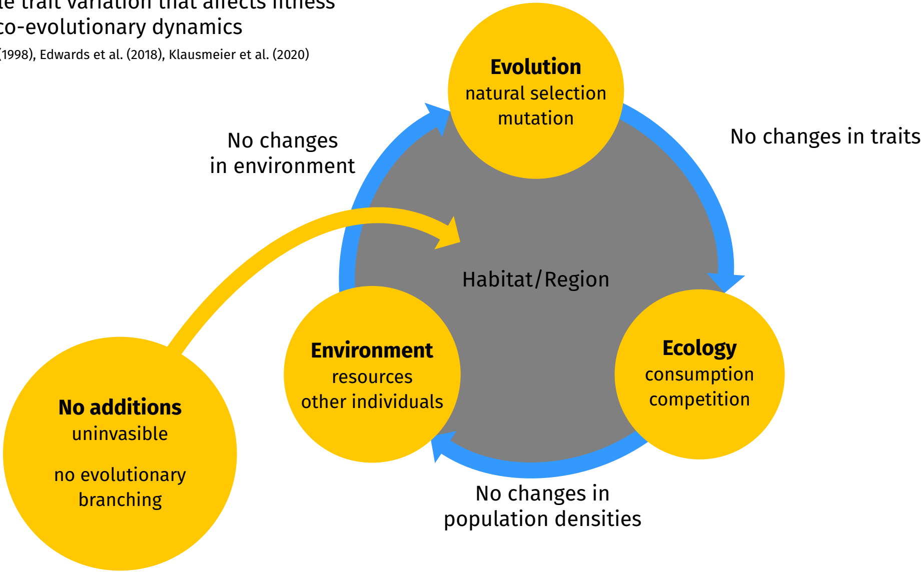

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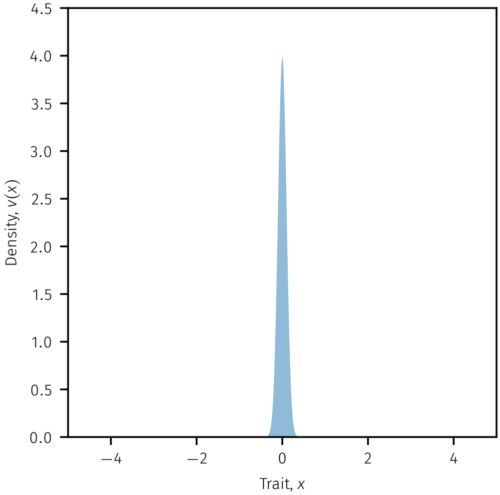
Strong stabilizing selection:



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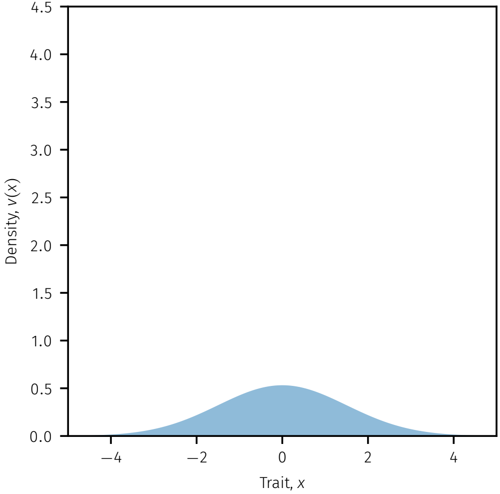

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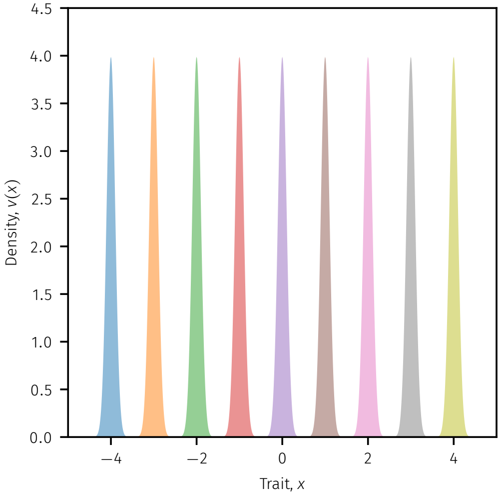

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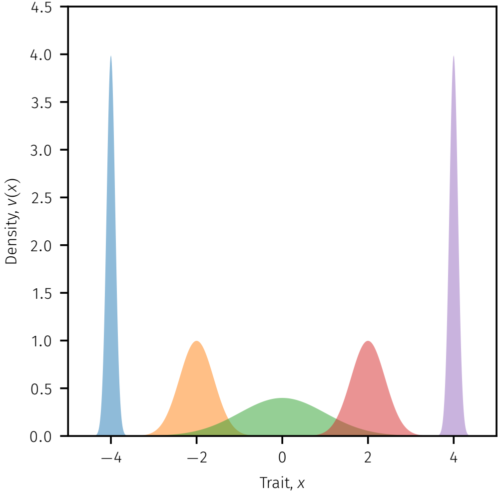

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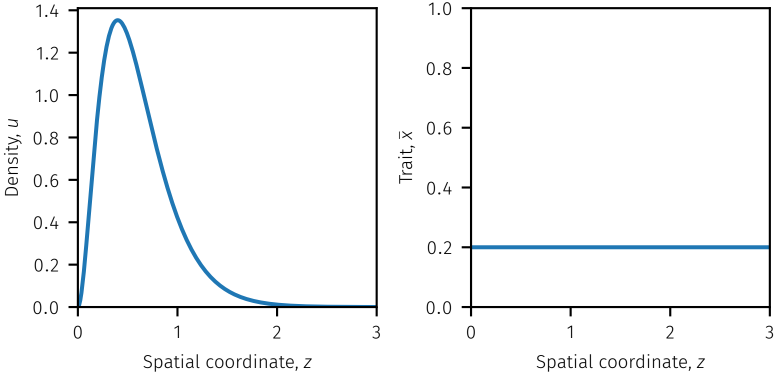
$$\frac{\partial u(z)}{\partial t} = \left[\text{local growth}\right] + \left[\text{random dispersal}\right]$$



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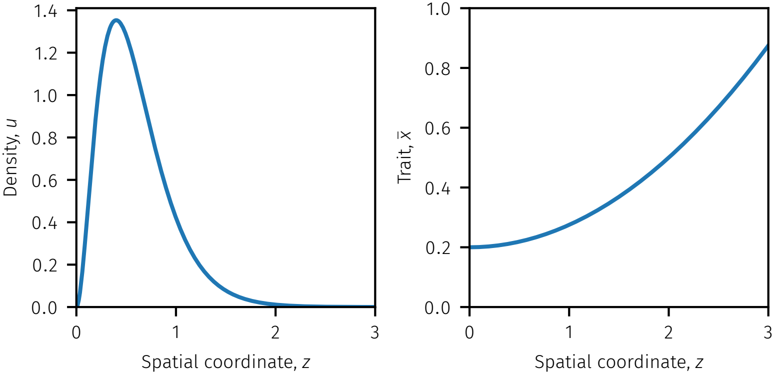

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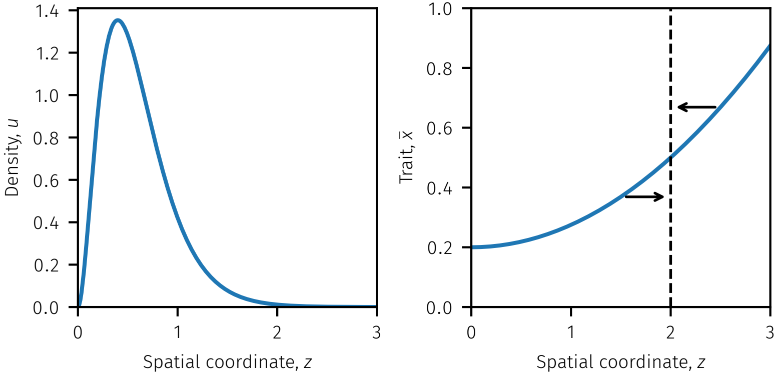

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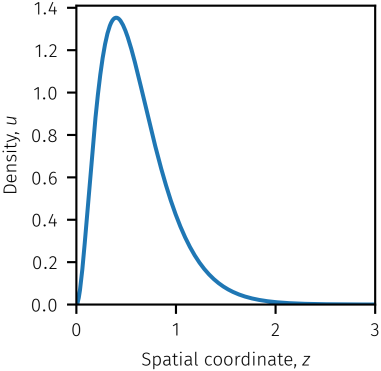

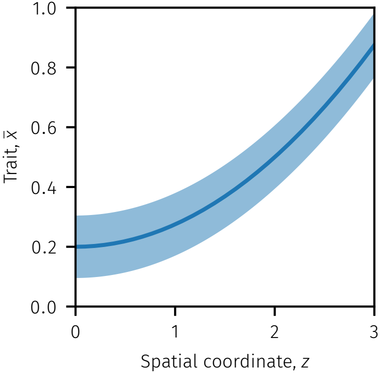

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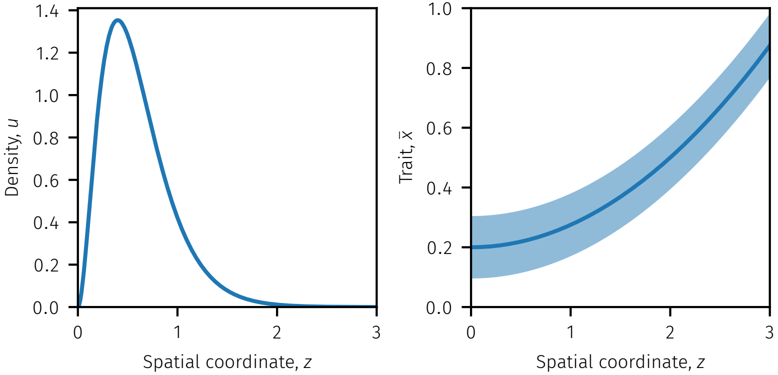

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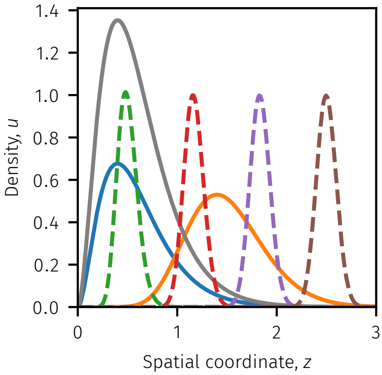
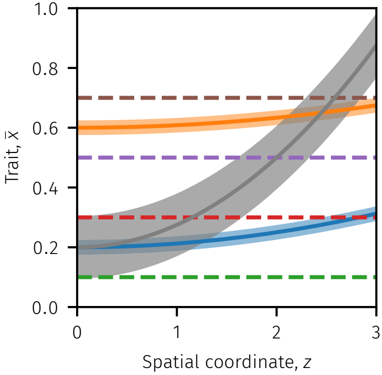
- Possible outcomes:
  - One species with much local adaptation
  - Many species with no local adaptation
  - Something in between





Theoretical frameworks

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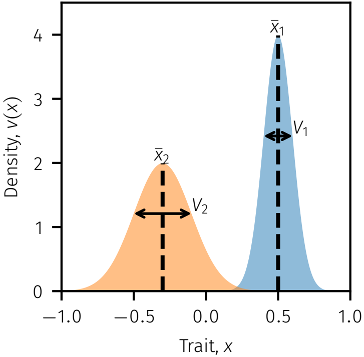
- Distirbution- and moment-based methods



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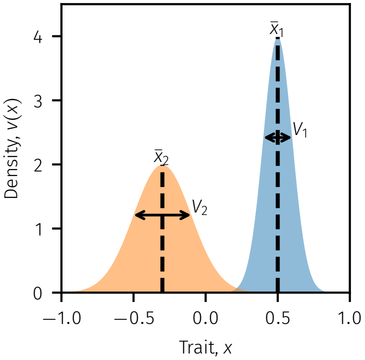

- **Quantitative genetics** (Lande, 1976), **Community ecology** (Wirtz and Eckhardt, 1996; Norberg et al., 2001), **Trait diffusion** (Merico et al., 2014; Le Gland et al., 2020), **Oligomorphic dynamics** (Sasaki and Dieckmann, 2011; Débarre et al., 2014; Lion et al., 2022)

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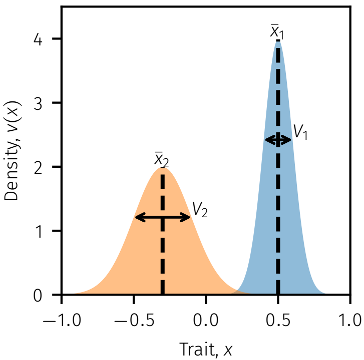

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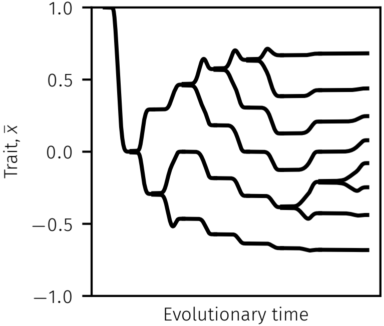

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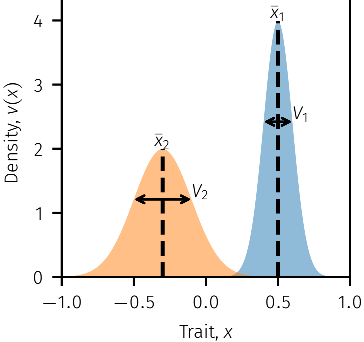

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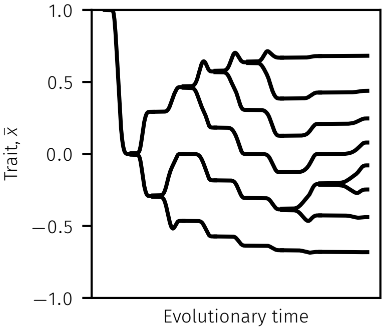

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Theoretical frameworks

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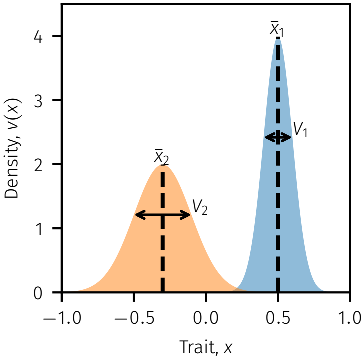

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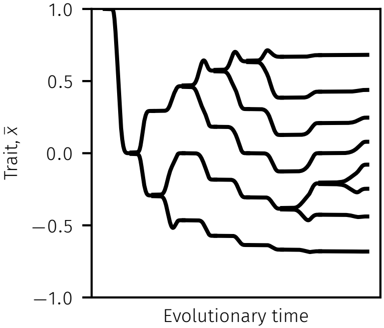

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Outline

- Introduce framework for combining intraspecific variation with eco-evolutionary invasion analysis and community assembly

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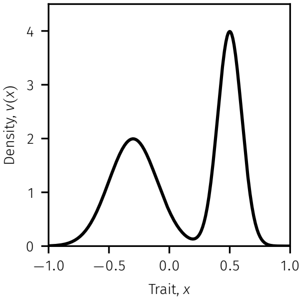
- Question 2: Investigate how trait variation is apportioned in ESCs within/between species and within/between patches as patches become more different in a two-patch Lotka-Volterra competition model

Trait-space and moment equations in unstructured communities

- $v(x)$



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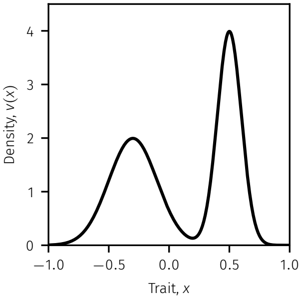

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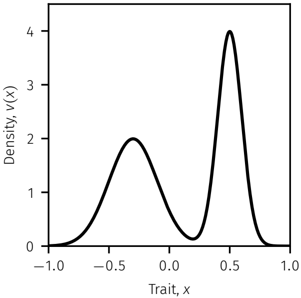

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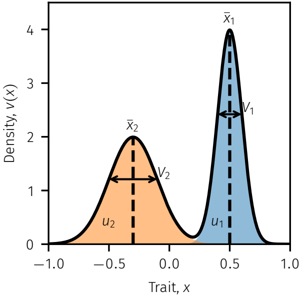

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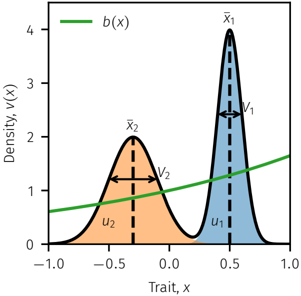
$$\hat{b}(\bar{x}, V, \tilde{v}) = \int_{-\infty}^{\infty} b(x, \tilde{v})\mathcal{N}(x, \bar{x}, V)\mathrm{d}x\,, \quad \hat{m}(\bar{x}, V, \tilde{v}) = \int_{-\infty}^{\infty} m(x, \tilde{v})\mathcal{N}(x, \bar{x}, V)\mathrm{d}x$$



$$b(x) = \exp(\alpha x) \implies$$

$$\hat{b}(\bar{x}, V) = \exp\left(\alpha\bar{x} + \frac{\alpha^2}{2}V\right)$$

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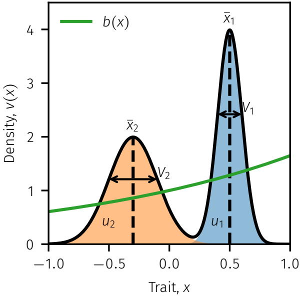
$$\frac{\mathrm{d}u_i}{\mathrm{d}t} = \left(\hat{b}(\bar{x}_i, V_i, \tilde{v}) - \hat{m}(\bar{x}_i, V_i, \tilde{v})\right) u_i$$



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Trait-space and moment equations in unstructured communities

- $v(x) = \underbrace{v_1(x) + v_2(x) + \ldots + v_S(x)}_{S\text{ ‘species’}} \approx \underbrace{u_1}_{\text{density}} \overbrace{\mathcal{N}}^{\text{normal}}(x, \underbrace{\bar{x}_1}_{\text{mean}}, \overbrace{V_1}^{\text{variance}}) + \ldots + u_S \mathcal{N}(x, \bar{x}_S, V_S) =: \tilde{v}(x)$
- Trait-space equations:

$$\frac{\mathrm{d}v(x)}{\mathrm{d}t} = \underbrace{\int_{-\infty}^{\infty} b(y,v)v(y)\mathcal{N}(x,y,M)\mathrm{d}y}_{\text{birth}*\text{mutation}} - \underbrace{m(x,v)v(x)}_{\text{mortality}}$$

- Moment equations ($i = 1, 2, \ldots, S$):

$$\hat{b}(\bar{x}, V, \tilde{v}) = \int_{-\infty}^{\infty} b(x,\tilde{v})\mathcal{N}(x,\bar{x},V)\mathrm{d}x\,, \quad \hat{m}(\bar{x}, V, \tilde{v}) = \int_{-\infty}^{\infty} m(x,\tilde{v})\mathcal{N}(x,\bar{x},V)\mathrm{d}x$$

$$\frac{\mathrm{d}u_i}{\mathrm{d}t} = \left(\hat{b}(\bar{x}_i, V_i, \tilde{v}) - \hat{m}(\bar{x}_i, V_i, \tilde{v})\right) u_i$$

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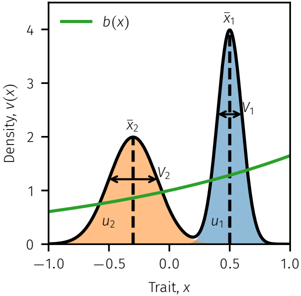

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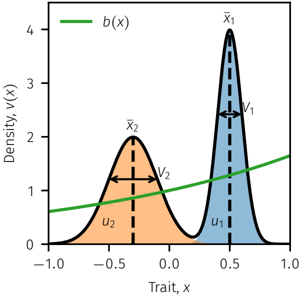

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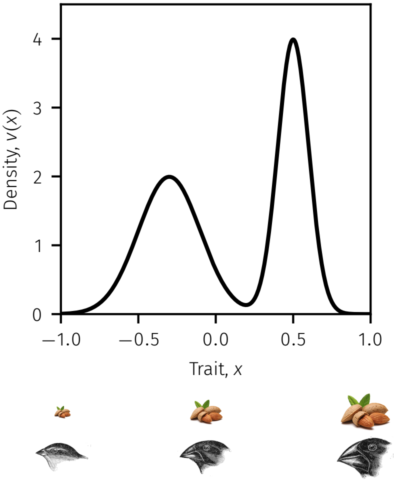
Example model—Lotka–Volterra competition

- Trait-density distribution $v(x)$



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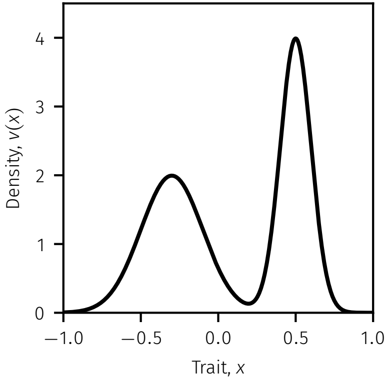

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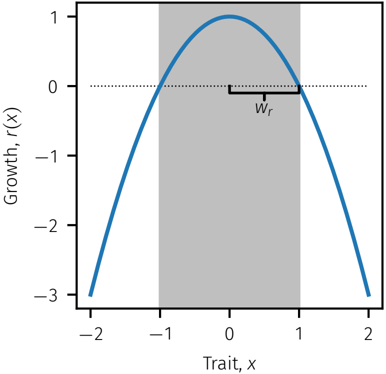

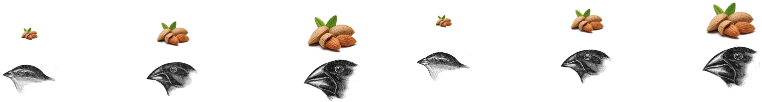

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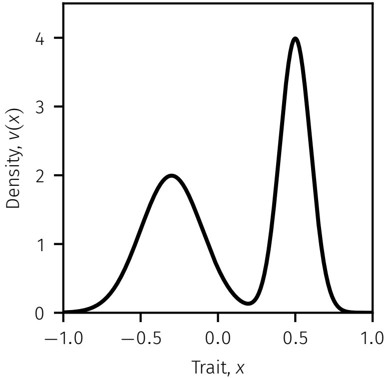

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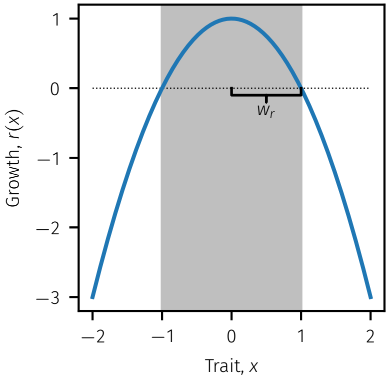
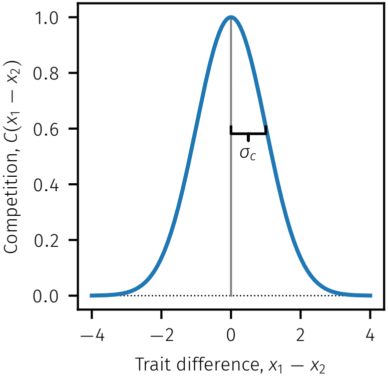
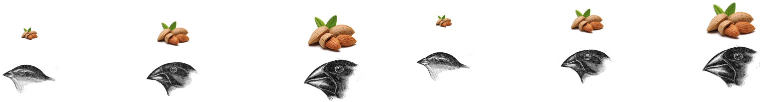
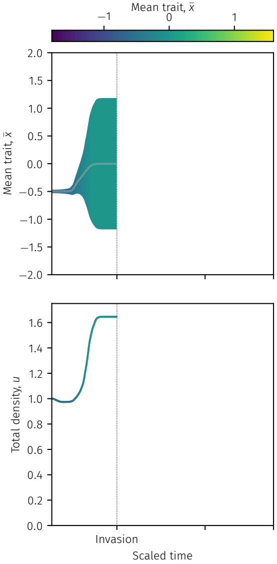






Community assembly



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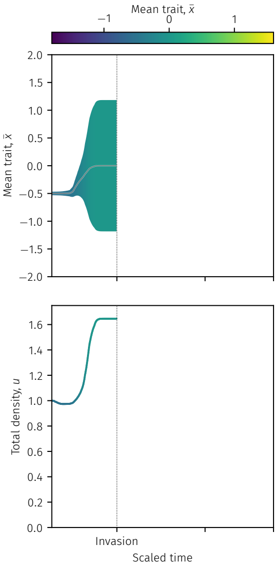

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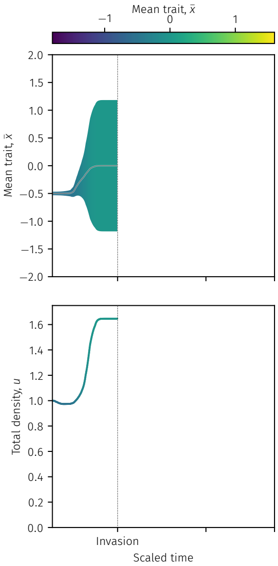

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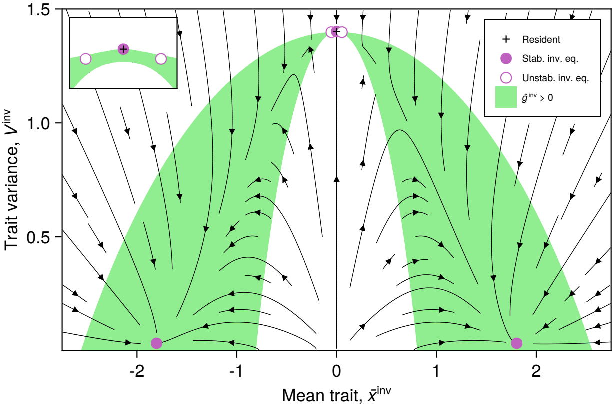

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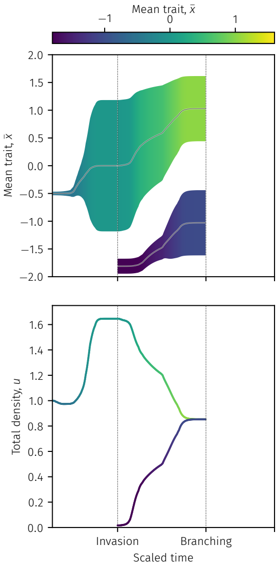

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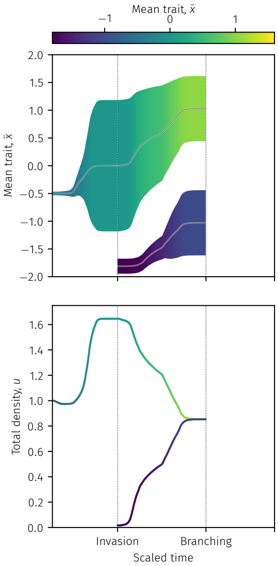

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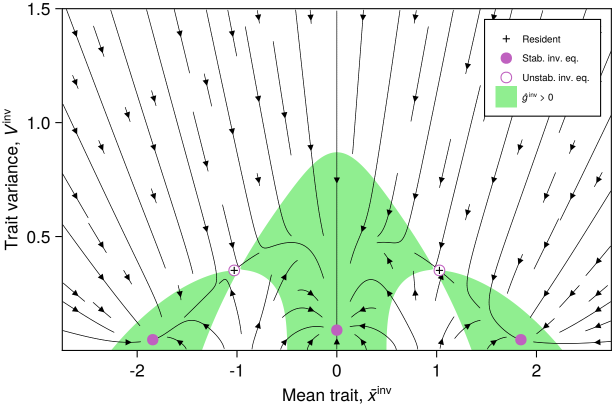

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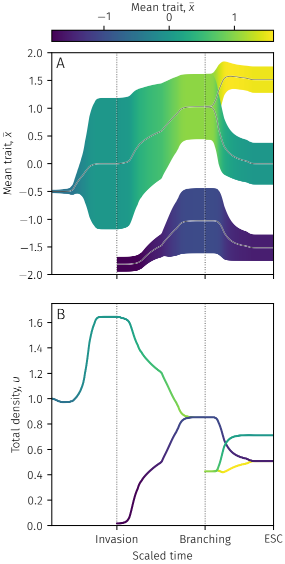

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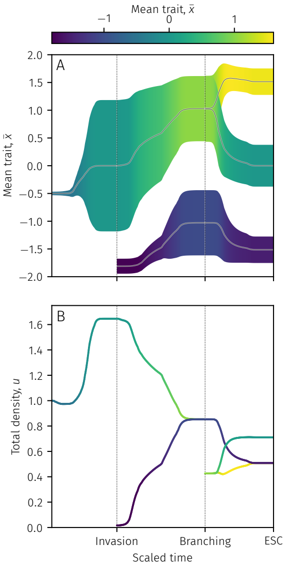

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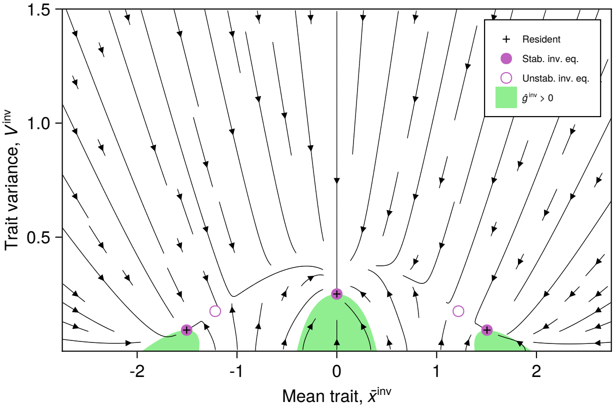
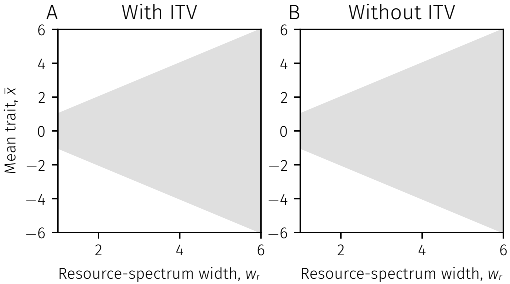


Question 1: What happens as selection becomes more disruptive?



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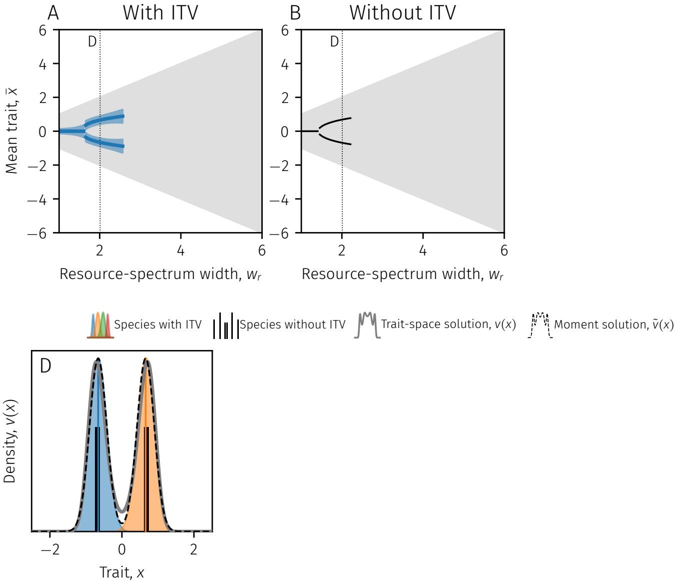

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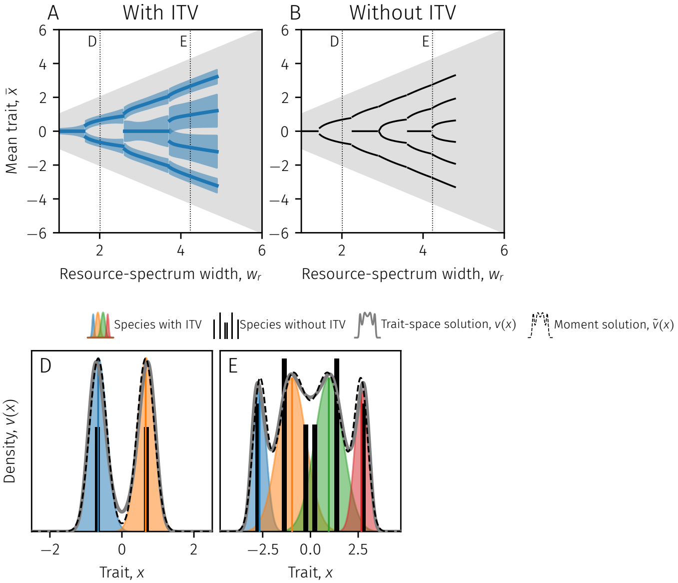

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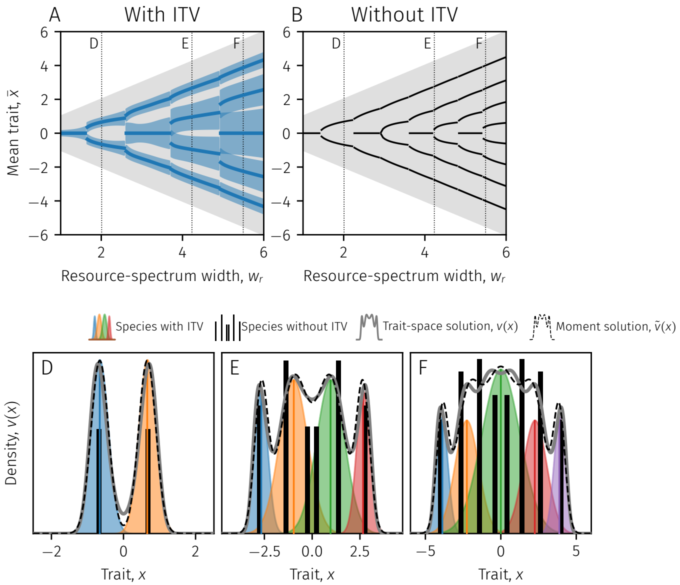

Structured populations

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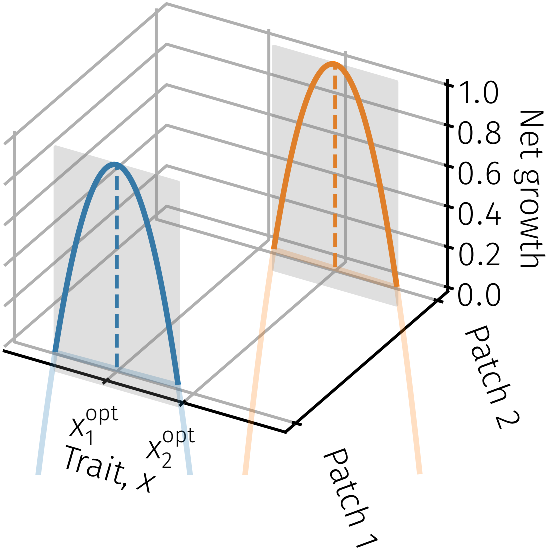

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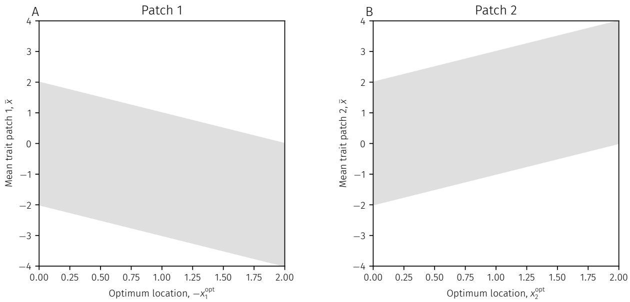

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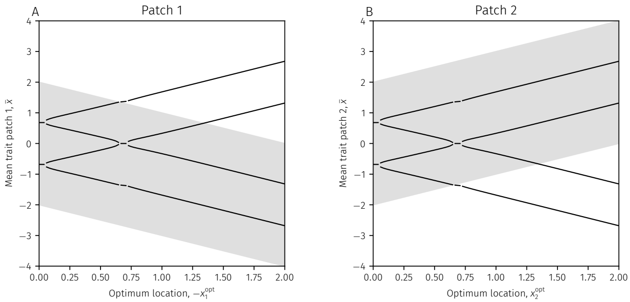

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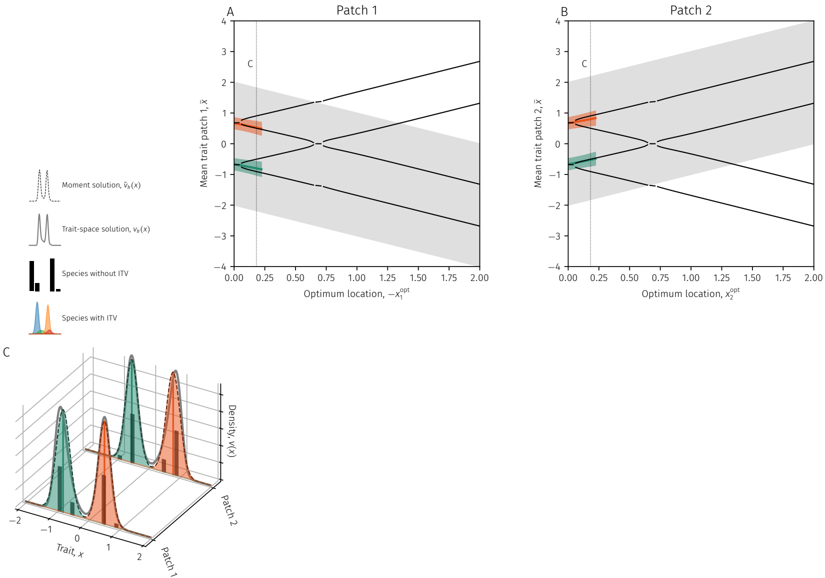

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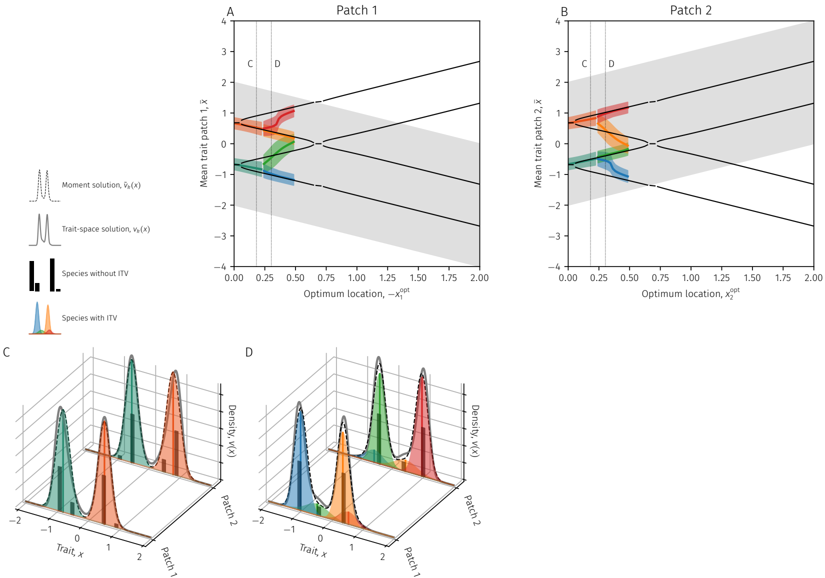

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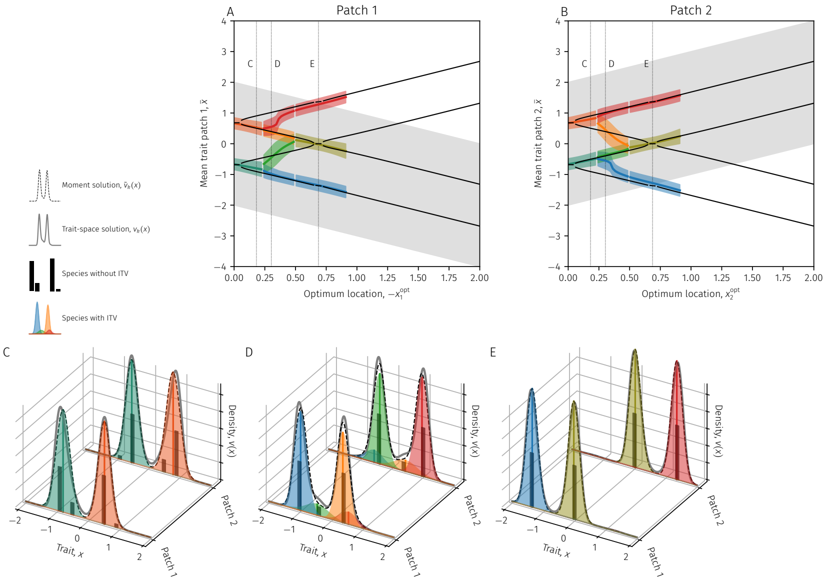

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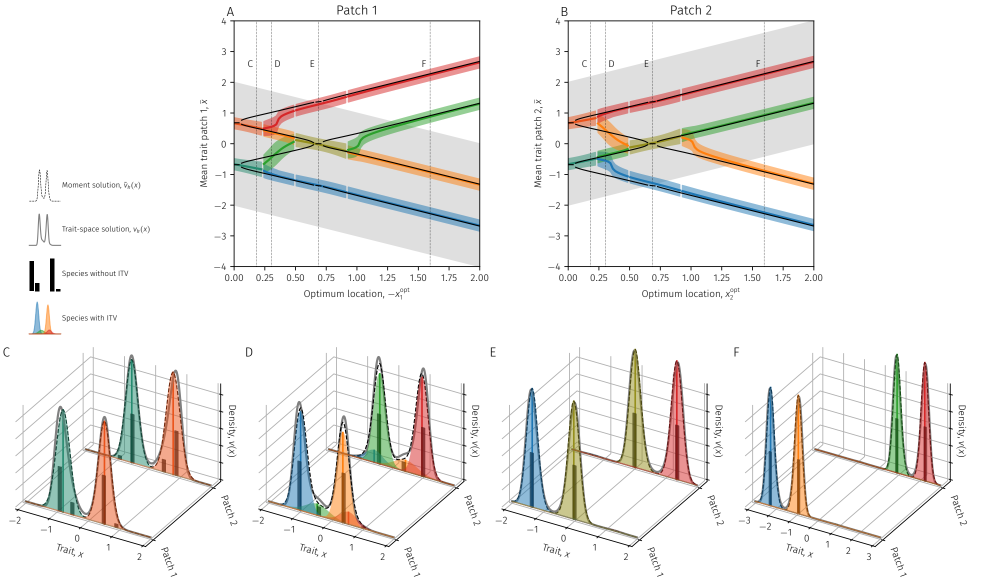

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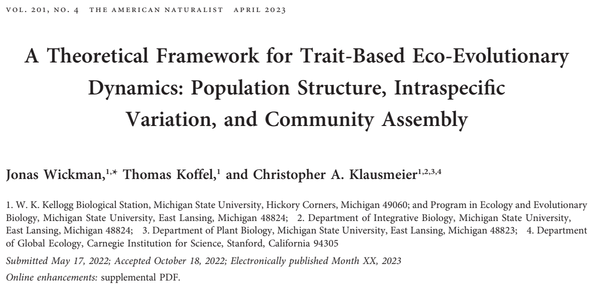
- Taking system specifics into account is necessary. Our framework can be used on the theory/modeling side to aid in this endeavor.

Thank you!



Paper available soon in *The American Naturalist*

Acknowledgments:

- Supported by NSF DEB-1754250 “Intraspecific Trait Variation in Phytoplankton at Different Scales” (PI Elena Litchman, co-PIs: CK, Ed Theriot)
- Thanks to American Naturalist editors Erol Akçay & Mike Cortez & 1 anonymous reviewer
- Check out paper by Sébastien Lion et al. :
  Lion S, Boots M, Sasaki A. 2022. Multimorph eco-evolutionary dynamics in structured populations. *American Naturalist* 200: 345–372

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Unstructured Lotka-Volterra equations

$$\frac{\mathrm{d}v(x)}{\mathrm{d}t} = \int_{-\infty}^{\infty} b(y)v(y)\mathcal{N}(y,x,M)\mathrm{d}y - \mu(x)v(x) - a(x,v)v(x)\,,$$

$$b(x) = r_0\,,\quad \mu(x) = \frac{x^2}{V_r}\,,\quad r(x) = b(x) - \mu(x) = r_0 - \frac{x^2}{V_r}\,,\quad a(x,v) = \int_{-\infty}^{\infty}\alpha(y,x)v(y)\mathrm{d}y\,,\quad \alpha(y,x) = \exp\left(-\frac{(y-x)^2}{2V_c}\right).$$

$$\frac{\mathrm{d}u_i}{\mathrm{d}t} = \Bigg[\underbrace{\left(r_0 - \frac{\bar{x}_i^2 + V_i}{V_r}\right)}_{\hat{r}(\bar{x}_i,V_i) = \hat{b}(\bar{x}_i,V_i) - \hat{\mu}(\bar{x}_i,V_i)} - \underbrace{\sqrt{2\pi V_c}\sum_{j=1}^{S} u_j\mathcal{N}(\bar{x}_i,\bar{x}_j,V_i+V_j+V_c)}_{\hat{a}(\bar{x}_i,V_i,\tilde{v})}\Bigg]u_i\,,$$

$$\frac{\mathrm{d}\bar{x}_i}{\mathrm{d}t} = V_i\Bigg[\underbrace{-\frac{2\bar{x}_i}{V_r}}_{\frac{\partial\hat{r}}{\partial\bar{x}}(\bar{x}_i,V_i)} + \underbrace{\sqrt{2\pi V_c}\sum_{j=1}^{S} u_j\frac{\bar{x}_i - \bar{x}_j}{V_i+V_j+V_c}\mathcal{N}(\bar{x}_i,\bar{x}_j,V_i+V_j+V_c)}_{-\frac{\partial\hat{a}}{\partial\bar{x}}(\bar{x}_i,V_i,\tilde{v})}\Bigg],$$

$$\frac{\mathrm{d}V_i}{\mathrm{d}t} = V_i^2\Bigg[\underbrace{-\frac{2}{V_r}}_{\frac{\partial^2\hat{r}}{\partial\bar{x}^2}(\bar{x}_i,V_i)} + \underbrace{\sqrt{2\pi V_c}\sum_{j=1}^{S} u_j\frac{V_i+V_j+V_c-(\bar{x}_i-\bar{x}_j)^2}{(V_i+V_j+V_c)^2}\mathcal{N}(\bar{x}_i,\bar{x}_j,V_i+V_j+V_c)}_{-\frac{\partial^2\hat{a}}{\partial\bar{x}^2}(\bar{x}_i,V_i,\tilde{v})}\Bigg] + \underbrace{r_0}_{\hat{b}(\bar{x}_i,V_i)}M\,.$$

Generic class-structured equations

$$\frac{\mathrm{d}v_d(x)}{\mathrm{d}t} \stackrel{\pm}{=} \int_{-\infty}^{\infty} f(y,\mathbf{v})v_s(y)\mathcal{N}(y,x,M)\mathrm{d}y\,, \qquad \mathbf{v}=(v_1,\cdots,v_K)$$

$$\frac{\mathrm{d}u_{id}}{\mathrm{d}t} \stackrel{\pm}{=} \overbrace{\hat{f}(\bar{x}_{is},V_{is},\tilde{\mathbf{v}})}^{\text{population-level per capita rate}}\,u_{is}\,, \qquad \hat{f}(\bar{x},V,\tilde{\mathbf{v}}) = \int_{-\infty}^{\infty} f(x,\tilde{\mathbf{v}})\mathcal{N}(x,\bar{x},V)\mathrm{d}x$$

$$\frac{\mathrm{d}\bar{x}_{id}}{\mathrm{d}t} \stackrel{\pm}{=} \overbrace{\frac{u_{is}}{u_{id}}}^{\text{relative-density weight}}\left[\underbrace{V_{is}\frac{\partial\hat{f}}{\partial\bar{x}}(\bar{x}_{is},V_{is},\tilde{\mathbf{v}})}_{\text{directional selection}} + \underbrace{\hat{f}(\bar{x}_{is},V_{is},\tilde{\mathbf{v}})(\bar{x}_{is}-\bar{x}_{id})}_{\text{mean-trait flow}}\right],$$

$$\frac{\mathrm{d}V_{id}}{\mathrm{d}t} \stackrel{\pm}{=} \overbrace{\frac{u_{is}}{u_{id}}}^{\text{relative-density weight}}\left[\underbrace{V_{is}^2\frac{\partial^2\hat{f}}{\partial\bar{x}^2}(\bar{x}_{is},V_{is},\tilde{\mathbf{v}})}_{\text{stabilizing/disruptive selection}} + \underbrace{\hat{f}(\bar{x}_{is},V_{is},\tilde{\mathbf{v}})(V_{is}-V_{id})}_{\text{trait-variance flow}} + \underbrace{\hat{f}(\bar{x}_{is},V_{is},\tilde{\mathbf{v}})(\bar{x}_{is}-\bar{x}_{id})^2}_{\text{between-to-within class variation}} + \underbrace{2V_{is}\frac{\partial\hat{f}}{\partial\bar{x}}(\bar{x}_{is},V_{is},\tilde{\mathbf{v}})(\bar{x}_{is}-\bar{x}_{id})}_{\substack{\text{class-local adaptation}\\ \text{and directional selection interaction}}} + \underbrace{\hat{f}(\bar{x}_{is},V_{is},\tilde{\mathbf{v}})M}_{\text{mutation}}\right].$$

Effects of mutation variance