

# Invasion and robustness in ecological meta-community models

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- ① Overview of ecological models.
- ② An eco-evolutionary meta-community model.
- ③ Some implications for stability analysis and applications.

# Ecological models: overview

We may be familiar with two-species predator-prey models:

Predator-prey model with logistic growth and Lotka-Volterra FR

$$\frac{dx}{dt} = rx(1 - x) - cxy, \quad \frac{dy}{dt} = \lambda cxy - dy$$

Generalising these relationships:

- **Community (foodweb) model:** multiple interacting species.  
Food chains; specialists vs. generalists.
- **Meta-population model:** single species, multiple patches.  
Environmental heterogeneity; dispersal.
- **Meta-community model:** multiple species, multiple patches.

Considerations for models of ecosystem development:

- How to define species (one vs. multiple traits)?
- How to specify the feeding relationships?
- Is network structure of the spatial landscape (regular, fractal, small worlds or large worlds) important?
- Can foodweb structure be generated by simple evolutionary rules with ecological feedback (**eco-evolutionary dynamics**)?

# An eco-evolutionary meta-community model

Species are defined by a bodysize and discrete set of traits that score against other traits. Begin with one species, and resources in each patch. Simulation occurs in nested loops:

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- **Evolutionary loop:** select parent species and introduce mutant (with 9/10 of parent's traits and similar bodysize).
  - **Ecological loop:** feeding, reproduction, death, dispersal.
    - **Foraging loop:** local populations select feeding strategies.

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Developed from the Webworld foodweb model (*Drossel et al* 2001).

# Ecological loop (feeding, reproduction, death, dispersal)

During ecological timestep  $t$ , population dynamics of species  $i$  in patch  $(x, y)$  updated:

$$N_{i,x,y}^t \mapsto N_{i,x,y}^t + \Delta \left( -2s_i^{-0.25} N_{i,x,y}^t + \lambda s_i^{-1} N_{i,x,y}^t \sum_{j=0}^n g_{i,j} s_j - \sum_{k=1}^n N_{k,x,y}^t g_{k,i} \right)$$

**Loss** due to mortality. **Gains** due to feeding. **Loss** due to predation.

$s_i$  is bodysize;  $\lambda = 0.3$  is ecological efficiency;  $g_{i,j}$  is functional response on  $j$

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Subsequently, migration **to** and **from** neighbouring patches:

$$N_{i,x,y}^t \mapsto N_{i,x,y}^t + \sum_{j=1}^{x_{\max}} \sum_{k=1}^{y_{\max}} \mu_{i,j,k,x,y} N_{i,j,k}^t - \sum_{j=1}^{x_{\max}} \sum_{k=1}^{y_{\max}} \mu_{i,x,y,j,k} N_{i,x,y}^t$$

Dispersal rate  $\mu$  increases in patches where population is declining.

# Foraging loop

Between updating population sizes, the local population of species  $i$  in patch  $(x, y)$  iterates feeding strategies in two stages:

- Update feeding efforts distributed across prey  $j$ :

$$f_{i,j,x,y} = \frac{g_{i,j,x,y}}{\sum_{k \in K_i} g_{i,k,x,y}}$$

- Update ratio-dependent functional responses:

$$g_{i,j,x,y} = \frac{S_{i,j} f_{i,j,x,y} N_{j,x,y}}{0.005 N_{j,x,y} + \sum_{k \in P_j} \alpha_{i,k} S_{k,j} f_{k,j,x,y} N_{k,x,y}}$$

$K_i$  is the set of possible prey of  $i$ ;  $P_j$  is the set of possible predators of  $j$ ;

$S_{i,j}$  is trait-dependent feeding score of  $i$  on  $j$ ;

$\alpha_{i,k}$  controls competition based on level of similarity.

# Example ensembles

Simulation generates a meta-community of co-evolved species.

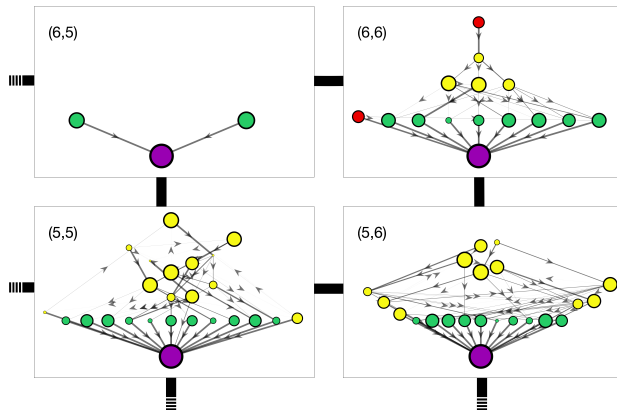
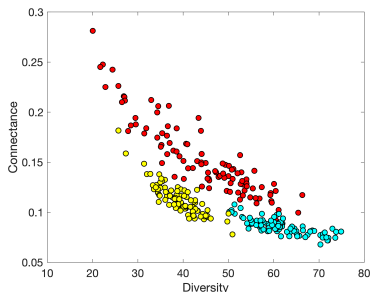


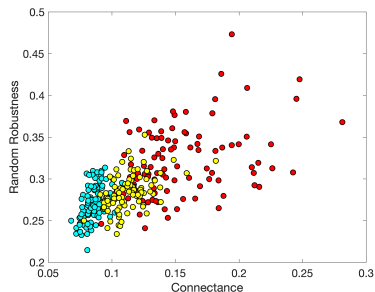
Figure 1: Foodwebs in  $6 \times 6$  spatial network (colours denote trophic role)



# Foodweb structure and stability



(a) Structure



(b) Robustness

Figure 2: Local foodweb properties (colours relate to model configuration)

- Scaling of number of feeding links  $L$  with number of species  $S$ .
- Connectance ( $L/(S(S - 1))$ ) decreases with diversity.
- Community robustness increases with connectance.

# Invasion of patches in the meta-community

Practical stability:  
**robustness** of existing  
ecosystems to species  
invasion.

Each species is deleted,  
(max loss 2.1%) then  
re-introduced to *all*  
patches (max loss 12%).

Number of patches  
invaded is increased by:

- Co-evolved traits.
- Larger bodysizes.

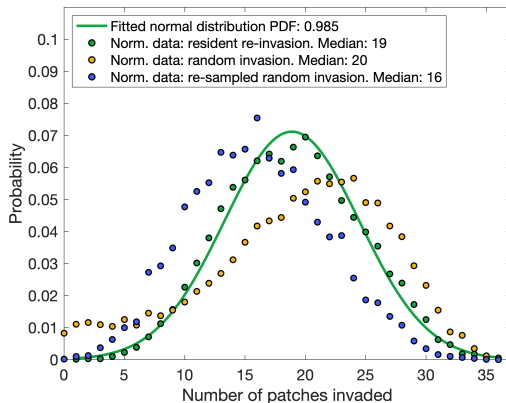
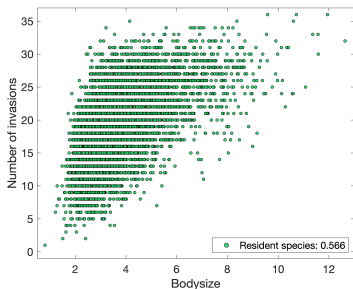
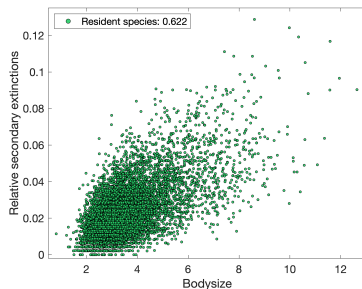


Figure 3: Probability of patch invasion

# Invasion - role of bodysize



(a) Patch invasions



(b) Secondary extinctions

Figure 4: Bodysize correlations with invasion and secondary extinctions

- Larger-bodysize species prefer to predate at higher trophic levels, avoiding strong competition to feed on resources.
- Benefit more from uniform-population re-introduction.

# Habitat loss and nature reserves

Patches are subjected to repeated random disturbances, except for 6 (of 36) designated as nature reserves. What is the best choice?

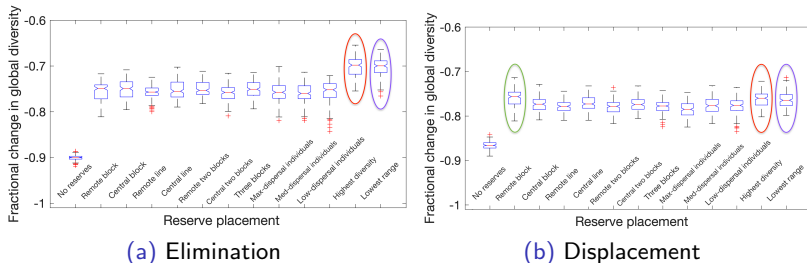


Figure 5: Biodiversity loss due to perturbation of random patch sequences

- Reliable to select patches with the **greatest biodiversity** or to protect the **rarest species**.
- If disturbed populations are displaced (rather than eliminated), isolating **large, remote areas** from invasion also effective.

## Summary:

- Models with simple evolutionary rules re-create complex network structure with greater stability.
- Can be used to determine principles for which sites and species are most vulnerable to perturbation, and hence inform environmental efforts.

## Challenges:

- Empirical data limited for validation.
- Abstract models hard to apply to specific ecosystems - focus on simpler, bespoke models?
- Exact mechanisms not easily identifiable in complex systems.

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- Abernethy, G. M. (2021). Sequences of patch disturbance in a spatial eco-evolutionary model. *Communications in Nonlinear Science and Numerical Simulation*, 97, 105746.