Modeling evolution of specialization – metapopulation aspect

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Put together:

- Adaptive dynamics approach
- Metapopulation models
- Mechanistically derived resource–consumer models
- Modeling trade-offs.

In order to understand:

- Evolution of specialization in resource utilization
- Evolutionary branching of dispersal
- Coexistence of specialists and generalists

- Origins of biodiversity.

Adaptive dynamics

- Assume that mutations are rare.

$\Rightarrow$ Resident population has reached an attractor when a mutant arrives.

$\Rightarrow$ It is possible to calculate *invasion fitness* for a mutant in an environment set by the resident population.

- Invasion fitness "=" expected number of offspring born to an average individual.
- In most ecological scenarios invasion fitness determines whether the mutant will oust the resident, coexist with the resident or vanish itself.

Metapopulation models

- The suitable habitat for a species is distributed to partially isolated patches.
- Each patch may support a local population.
- Local populations have dynamics of their own but are connected by dispersal.
- Random local catastrophes may eradicate local populations (but the patch remains habitable and is possibly recolonized by dispersers).
- Invasion fitness ”=” Expected number of new successful dispersers sent out by the clan initiated by an average disperser.

Metapopulations and specialization

- Species live in fragmented landscapes.
- Resource availabilities are different in different habitats.
- Adaptation to certain local conditions may even be harmful at the metapopulation level.

$\therefore$ Metapopulation aspects should be taken into account when analyzing the evolution of specialization.

This presentation shows how to derive metapopulation models that

- are mechanistically based on individual level ingredients.
- allow the evolutionary analysis of specialization (and dispersal) using the adaptive dynamics approach.

Agenda

1. **1.** Formulate a continuous-time within-season dynamics for consumers and two alternative resources.
2. **2.** Derive a discrete-time between-season model for the consumer populations.
3. **3.** Lift the model to the metapopulation level.
4. Show how to calculate fitness values in this metapopulation model.
5. Study the evolution of specialization (and dispersal).

Definitions and notations

First derive local within-season dynamics for the density $x_n(t)$ of a single consumer species:

- $R_n^i(t) =$ The density of resource i at time $t \in [0, 1]$ during period $n = 1, 2, 3, \ldots$.
- Individuals consume the resources 1 and 2 according to the law of mass action with efforts β_1 and β_2.

Definitions and notations

- The consumers use resources to produce new eggs. Only the eggs survive to next season.
- The new population is formed from those eggs that hatch successfully.
- $E_n(t) =$ The egg density.
- The resources have chemostat dynamics with carrying capacities K_i.

Within-season dynamics

$$(\varepsilon)\frac{dR_n^i}{dt}(t) = \alpha\left(1 - \frac{R_n^i(t)}{K_i}\right) - \beta_i R_n^i(t) x_n(t)$$

$$\frac{dE_n}{dt}(t) = \gamma\left(\beta_1 R_n^1(t) + \beta_2 R_n^2(t)\right) x_n - \delta E_n(t),$$

$$x_{n+1}(0) = \rho E_n(1)$$

$$E_n(0) = 0$$

The dynamics of different resources interact only via shared consumers.

Within-season dynamics II

For simplicity assume:

- $x_n(t) \equiv x_n(0) := x_n$ (no within-season adult mortality).
- ε is small (resource dynamics is fast compared to consumer dynamics and is always on a quasi-equilibrium).

Scaling without loss of generality:

- $\alpha = 1$

Local between-season dynamics

For a single strategy s consumer species the discrete-time dynamics is:

$$x_{n+1} = \lambda x_n \left(\frac{K_1 \beta_1}{1 + K_1 \beta_1 x_n} + \frac{K_2 \beta_2}{1 + K_2 \beta_2 x_n} \right)$$

$\therefore$ The Beverton–Holt model.

Local between-season dynamics

For several consumers this generalizes to:

$$x_{n+1}^{(j)} = \lambda x_n^{(j)} \left(\frac{K_1 \beta_1^j}{1 + K_1 \sum_k \beta_1^k x^{(k)}} + \frac{K_2 \beta_2^j}{1 + K_2 \sum_k \beta_2^k x^{(k)}} \right)$$

- Explicit definition of the trade-off necessary to analyze evolution of specialization.

Trade-off

Let strategy $s \in [0, 1]$ of an individual to determine the degree of specialization.

- $s = 1 \iff$ specialist on resource 1.
- $s = 0 \iff$ specialist on resource 2.
- $s = 0.5 \iff$ unbiased generalist.

Trade-off function

Assume that there is an increasing function $\beta : [0,1] \longrightarrow \mathbb{R}$ such that

- $\beta_1 = \beta(s)$ and $\beta_2 = \beta(1-s)$ ("identical resources").
- $\beta(0) = 0.$
- $\beta(1) = 1$ (scaling without loss of generality).

Trade-off function

The choice of function β is essential for the evolutionary dynamics of specialization.

- Dieckmann & Mazancourt
- $\beta(s) = s \Longleftrightarrow$ Strategy corresponds, for example, to search time allocation.

Trade-off function

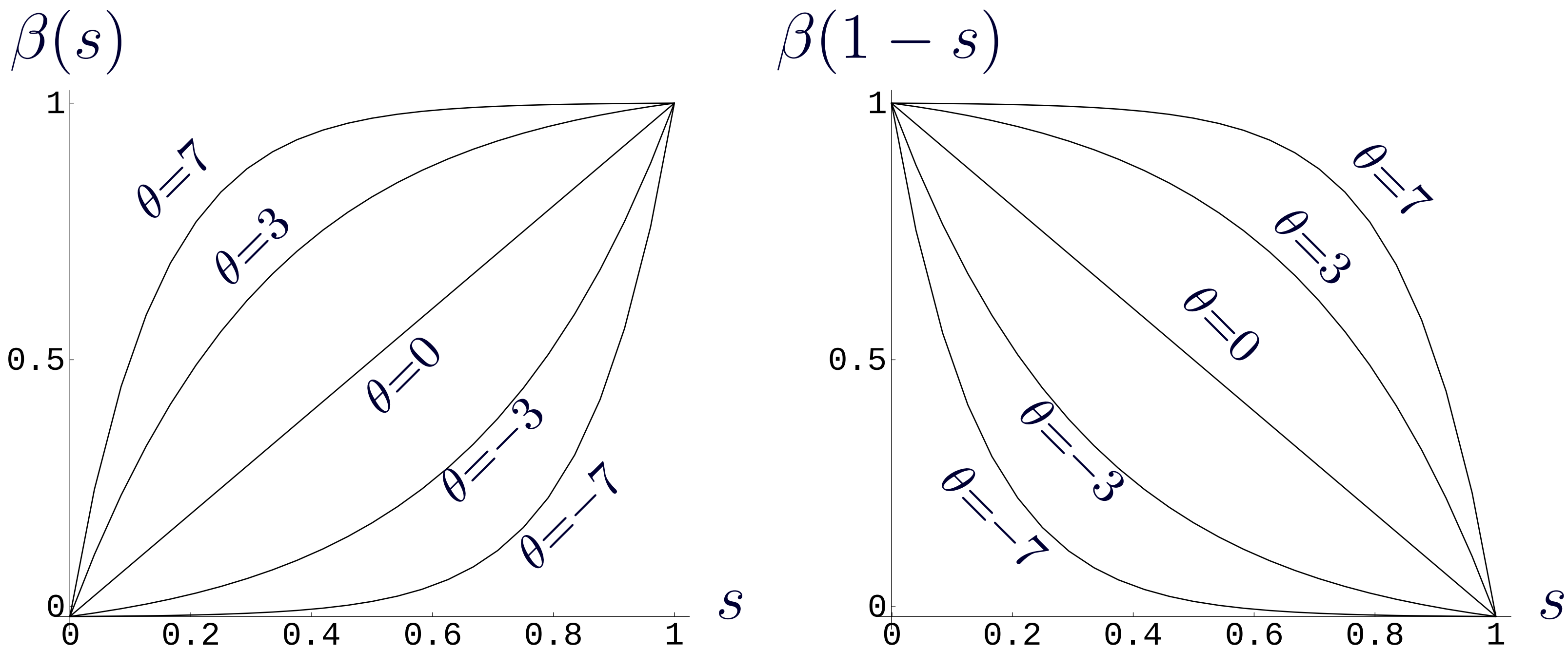
More general definition using trade-off parameter θ:

$$\beta(s) = \frac{1 - e^{-\theta s}}{1 - e^{-\theta}}, \qquad \theta \neq 0.$$

$$\beta(s) = s, \qquad \theta = 0.$$

$\theta > 0 \iff$ Additional benefit of generalism.
$\theta < 0 \iff$ Additional cost of generalism.

Trade-off function



Resource consumption function β for different values of the trade-off parameter θ.

Hitherto and next

- A simple continuous-time resource consumption model for two resources has been constructed.
- This model has been used to derive a discrete-time population model.
- Next this model will be generalized to the metapopulation level.

The metapopulation level

- Infinitely many habitat patches, finitely many patch types.
- All patches equally connected via dispersal pool.
- Random local catastrophes may destroy populations.
- Each local patch exhibits its own discrete-time population dynamics. (Deterministic dynamics $\Leftrightarrow$ Large local populations.)

The metapopulation level – Notations

Fecundity of a strategy s individual in a type m patch is

$$\begin{aligned} f^m(s, S_n, X_n) &= \lambda\left(\frac{K_1^m \beta(s)}{1 + K_1^m \sum_j \beta(s_n^{(j)}) x_n^{(j)}}\right. \\ &+ \left.\frac{K_2^m \beta(1-s)}{1 + K_2^m \sum_j \beta(1 - s_n^{(j)}) x_n^{(j)}}\right), \end{aligned}$$

- $S_n =$ the vector of strategies present in the patch at time n
- $X_n =$ the vector of corresponding populations sizes.

The metapopulation level – Notations

- $e =$ the probability that an individual emigrates.
- $\pi =$ the probability that an emigrant survives dispersal
- $D_n(s)$ the dispersal pool size of strategy s dispersers at time n.

The metapopulation level – Notations

Local catastrophes:

$$C(n+1) = \begin{cases} 0, & \text{if a catastrophe occurs at period } n \text{ (prob. } c\text{).} \\ 1, & \text{if no catastrophe at period } n \text{ (prob. } 1-c\text{).} \end{cases}$$

The metapopulation dynamics

The local population size of strategy s in a type m patch:

$$x_{n+1} = C(n+1)(1-e)f^m(s, S_n, X_n)x_n + \pi D_n(s).$$

The size of the disperser pool (heuristically):

$$D_n(s) = \sum_m p_m \left(\begin{array}{l} \text{Expected number of strategy } s \text{ emigrants} \\ \text{from a type } m \text{ patch at time } n \end{array} \right).$$

How to find metapopulation attractor I

1. Note, that the Beverton–Holt model only exhibits fixed point dynamics and the same holds for this metapopulation model.
2. There exists a unique combination of disperser pool sizes $D(s)$ towards which the state of the metapopulation converges (quasi-equilibrium).

How to find metapopulation attractor II

3. Assume that each disperser pool size $D_n(s)$ has constant value $D(s)$.
4. Calculate iteratively all the population sizes in the patches as a function of the time since the latest catastrophe:

$$x_{n+1} = (1-e)f^m(s, S_n, X_n)x_n + \pi D(s).$$

How to find metapopulation attractor III

5. Calculate how many new successful disperser is in average produced by a strategy s disperser immigrating into a type i patch η time units after the latest catastrophe.
6. Sum over all values of η and i to calculate how many successful dispersers is produced by an average strategy s disperser. In equilibrium this value must be exactly 1 for all strategies present in the metapopulation.

How to find metapopulation attractor IV

7. Solve the actual values of the disperser pool sizes $D(s)$ for each resident strategy from a fixed point equation.
8. Calculate iteratively the real resident population dynamics for each resident strategy and patch type.

The metapopulation dynamics – Mutant fitness

- Once the resident dynamics are known, one can calculate how many new successful dispersers an average mutant disperser is expected to produce.
- This value can be used to deduce the mutant fitness.

Conclusions

- In order to analyze the relation between dispersal the evolution of specialization, models with finite number of patches (no catastrophes) are insufficient since catastrophes affect this relation notably.
- Specialization affects even qualitatively the evolution of dispersal.
- Analyzing joint evolution of dispersal and specialization is necessary in order to understand the evolution of specialization.
- Joint evolution enables evolutionary path to the coexistence of generalists and specialists.

Thank You for Your Attention!