Schoener Review

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1. Predation

1.1. *Models*

The basic predation model with TYPE I (linear) predator response to prey

$$\frac{\mathrm{d}F}{\mathrm{d}t} = rF - \alpha FN \tag{1}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \beta\alpha FN - DN \tag{2}$$

is neutrally stable. Adding LOGISTIC GROWTH, MacArthur (1970), (1972), notation by Schoener (1974), in prey F tips this to a single stable point. May either spiral in (if D or K is large), or move in directly.

$$\frac{\mathrm{d}F}{\mathrm{d}t} = rF\left(1 - \frac{F}{K}\right) - \alpha FN \tag{3}$$

If instead we shift the TYPE II response $g(f)$ to model predator saturation, this makes the singular point unstable,

$$\frac{\mathrm{d}F}{\mathrm{d}t} = rF - \alpha g(F)N \tag{4}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \beta\alpha g(F)N - DN \tag{5}$$

$$g(F) = \frac{F}{U + F} \tag{6}$$

Since releases prey from control. Stronger nonlinearity when U is small, meaning long handling times h relative to search times, so $U \propto \frac{T_s}{h}$. Critiques include Jeschke et al. (2002) observe Type II derivation doesn't include state dependence (predator satiation) or uncertainty (some attacks fail). [1]

Using instead a TYPE III response

$$g(F) = \frac{F^a}{U^a + F^a} \tag{7}$$

in (4), (5), coexistence is only stable when per capita risk increases with prey density, implies $\frac{\mathrm{d}g(F)}{\mathrm{d}F} > \frac{g(F)}{F}$, Oaten & Murdoch (1975). More likely when equilibrium prey density small. Type III response can occur due to prey switching, Van Baalen et al. (2001).

1.2. *Experiments*

- Luckenbill (1973), analyzed by Harrison (1995): Matches predictions for first three models. (a) The original population oscillates to accidental extinction, (b) decreased nutrition/carrying capacity of F (*Paramecium*) stabilizes, (c) methyl cellulose lengthens search time T_s, increasing U, stabilizing effect. [2]
- PREDATOR-PREY OSCILLATIONS: Lynx-Hare, Krebs et al. (1995) 8-yr study, food addition and predator exclosures both increase hare density independently, synergistic when combined. Still observe cycles of same magnitude but higher average. Forest Lepidoptera cycle, Turchin et al. (1993) explains well with parasitoid model alone.

2. Competition

2.1. *Basic Lotka-Volterra Model*

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = rN_i(1 - \alpha_{ii}N_i - \alpha_{ij}N_j) \tag{8}$$

Stable coexistence if $\alpha_{ii} > \alpha_{ij}$, linear isoclines. [3] Can get competitive exclusion of the inferior species, or a SEPARATRIX representing FOUNDER CONTROL, where the more abundant species always wins. Experimental laboratory tests summarized in Table 1.

Critiques of the basic model include

(i) Pairwise competition does not predict behavior in a full community of many species (see Table 1), also section 2.4 and Food Webs, section 7.
(ii) Inter and intraspecific competition intensities (α's) themselves depend on species density. See Nonlinear isoclines, section 2.2.
(iii) Resources not modeled and not dynamic, For an example, see Tilman (1977) chemostat model, and section 2.4.
(iv) Competition not necessarily mechanistic, but see Crowley (2005) and section 2.3.

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[1] Derivation aside, Type II offers a simple saturating response. Both the objections simply increase the ease of that saturation, and make it more destabilizing.

[2] Some argue Type III fits data better, but mechanism makes sense for II and not for III, besides which III has an extra parameter anyway.

[3] Isoclines have slope $\frac{\alpha_{ii}}{\alpha_{ij}}$, hence steeper slope isocline is the one belonging to the x-axis variable when coexistence occurs.

Reference	Organism	Coexist	Fits LV?
Gause (1934)	Yeast, *Paramecium*	No	Yes
Park (1962)	*Tribolium*	No	Yes (saddle)
Vandermeer (1969)	4 sp of *Paramecium*	Yes	Qualitative fit only
Neill (1974)	many microcrustacean sp	Yes	Pairwise α_{ij}'s depend on other sp.
Gilpin & Ayala (1976)	*Drosophila*	Yes	LV predicts saddle, need nonlin isoclines

Table 1
Lab Experiments on Competition

2.2. *Nonlinear isoclines model*

Allow some combination of the terms in this model, Schoener (1974), (1976), (1978).

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = rN_1 \Bigg(C - \underbrace{\alpha_{11}N_1}_{\text{intraspecific}} - \underbrace{\alpha_{12}N_2}_{\text{interspecific}} +$$
$$\underbrace{\frac{I_{O1}}{Y_1 + N_1 + \beta N_2}}_{\text{overlapping}} + \underbrace{\frac{I_{E1}}{Y_1 + N_1}}_{\text{exclusive}} \Bigg) \quad (9)$$

In addition to the behaviors from before, we can now get multiple stable states Gilpin & Ayala (1976).

2.3. *Mechanistic Models*

– Crowley et al. (2005): A mechanistic LV model of competition for space

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = b_1 N_1 (1 - N_1 - N_2) - d_1 N_1 + c N_1 N_2 \quad (10)$$

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = \underbrace{b_2 N_2 (1 - N_1 - N_2)}_{\text{colonize open area}} - \underbrace{d_2 N_2}_{\text{death}} - \underbrace{c N_1 N_2}_{\#2 \text{ loses overlap}} \quad (11)$$

All classic LV results possible, coexisting when trade-off between growth rates and competition. Observational evidence in many systems, including crustose algae, male and female liverworts, lichens species.
– Tilman (1976) (Titman): Species that can suppress limiting resource to lowest level R^* wins. Coexistence requires same number of resources as consumers, and that each species growth rate is limited by a different resource. Essential to model resource abundance explicitly, since results depend entirely on resource's dynamic equilibrium, R^*.
– Mechanistic derivations of the α_{ij} *in standard LV model*, Eq (8), from resource overlap, MacArthur & Levins (1967), coining the term LIMITING SIMILARITY. Schoener (1974) modification: electivity ratio d/f to distinguish between consumed vs available resources. In so doing, MacArthur launches a new theory of niches and limiting similarity, section 3.

2.4. *Challenges of Multispecies Competition*

Case (1995) Transients matter – an invader can enter and subsequently go extinct, but drastically changing community composition. Huisman & Wessing (2001) Multispecies LV with explicit resources model very unpredictable. Roelke et al. (2003) demonstrate by simulation and experiment that pulsing resources make the model very predictable.

2.5. *Experimental Evidence*

Laboratory experiments summarized in Table 1. Sample field experiment is Petren & Case (1996), demonstrating EXPLOITATIVE competition in geckos: showed resource use overlaps, each negatively impacted abundance of the other, with no evidence for interference. Schoener (1983) review finds ample field evidence for competition.

3. Limiting Similarity and Niche Partitioning

3.1. *Limiting Similarity*

– MacArthur & Levins (1967), uses predation model equilibrium with consumers Eq (2), and resources (3) to justify the distribution model of the niche for Lotka-Volterra (8) competition between consumers. Introduces term limiting similarity, Gaussian kernel view of the niche, and d/w theory. Much follow up assumes the same LV model.
– Roughgarden (1974) Changes resource distribution from Gaussian. Peaked (leptokurtic) can pack more species, flat (platykurtic) can pack less, Yoshiyama & Roughgarden basically same with higher dimensions. dding stochasticity: May & MacArthur (1972) destabilize, vs. Turelli (1981) can make invasion easy or harder when large, unimportant when small (as predicted by Abrams 1975).
– Abrams (1975) Shows that non-LV models can show tighter packing, no similarity barrier! Roughgarden & Feldman (1975) Frequency dependent predation allows arbitrary packing, (but optimal diet theory says predation not frequency dependent).

3.2. *Niche Partitioning*

– Schoener (2008) review: Grinell (1917) a role in community. Hutchinson (1957) n-dimensional hypervolume in which persistence possible, $r > 0$. Fundamental vs realized niche. MacArthur & Levins (1976) resource utilization curves. Ecological Niche modeling, GIS based methods like MaxEnt.
– **Experiments** McKane et al. (2002) all plants prefer best nitrogen (N) source, but when grown together partition to use different nitrogen sources. Impacts productivity, community structure, realized vs fundamental niche. Chase & Belovsky (1994) consider included niche model (a specialist whose resources are also used by a generalist with a curved isocline). Predictions match experimental data with two grasshopper species.

4. Null Models

Review in Gotelli & Graves (1996). Common in identifying community-level patterns: community assembly rules, extinction,

evolution, diversity. Ask if pattern (i.e. distributions of sizes observed in community) could have occurred by chance.

5. Character Displacement

The evolutionary response to limiting similarity:

5.1. *Models*

Abrams (1986) Differential equation model, can traits can diverge, parallel, or specialist and generalist can converge. Taper & Case (1985) Quantitative genetics model with resource utilization distributions and resource availability distributions.

5.2. *Experimental*

Criteria Schluter (2000): (1) genetic basis, (2) not by chance, (3) not species sorting, (4) trait must effect resource use, (5) not from environmental differences between allopatry and sympatry (6) independent evidence for competition. Examples

- Fenchel (1975) In sympatry, small and large snails, while usually only one size when in separated fjords. Size determines food source. However, later work showed response is plastic (could be duplicated in single generation by taking both allopatric populations into sympatry in lab).
- Schluter (1994) Limnetic sticklebacks grown with hybrids, compare to hybrids grown without limnetics. The more benthic ones perform better when mixed with limnetics, relative to the more benthic hybrids without limnetics. Critique by Murtaugh et al. (1995) on hybrids, not controlled by density, etc. Schluter (2000) repeats with benthic and hybrid mix as well as limnetic-hybrid mix, addressing density issue, etc. Rundle et al. (2003) character displacement stronger under predation.

6. Three-way interactions

6.1. *Apparent Competition*

An example of an INDIRECT EFFECT in a food web, which can sometimes play very important roles, Abrams et al. (1996).

- **Models** Holt (1977) introduces term, basic model, Holt (1987) predicts importance of aggregative response.
- **Experiments** Schmitt (1987) Aggregating bivalves and gastropods increases predation on both. Chaneton & Bonsall (2000) review, find most cases very asymmetric, more (0,-) than (-,-) response. Probably due to very different relative abundances.

6.2. *Intraguild Predation*

As summarized in review, Polis et al. (1989),

- **Types**: Tend to be AGE-STRUCTURED but symmetric: all fish eat zooplankton young of other fish, or unstructured but ASYMMETRIC: spiders eat insects, lizards eat spiders and insects. A unstructured symmetric example: black widows can catch scorpions in webs, but scorpions can eat them on the ground.

- **Consequences**. *Communities* can face alternate stables states: lobsters eat predatory snails. If no lobsters, snail density gets high enough and they can eat any invading lobster. *Populations* may look more like competition if common prey is abundant and intragulid prey rare, or more like predation otherwise. *Individuals* may face niche shifts, behavioral changes, etc.

7. Food Web Complexity

Models: Yodzis (1988) Press perturbation adds immigration term to the community dynamics, $\frac{dN_i}{dt} = f_i(N) + I$, which can be thought of as a small perturbation from equilibrium, $0 = f_i(N(I)) + I$. Differentiating with respect to I (chain rule), $0 = \frac{\partial f_i}{\partial N_j} \frac{\partial N_j}{\partial I} + 1$. Since at equilibrium the $\frac{\partial f_i}{\partial N_j} = A_{ij}$ is the community matrix (Jacobian), rearranging gives us

$$\frac{\partial N_i}{\partial I_j} = -(A^{-1})_{ij} \tag{12}$$

Uses this to argue that most ecological interactions will be indeterminate as perceived through perturbation experiments.

Experiment: Schmitz (1997) Parameterize and computed Yodzis community matrix for familiar system of grasshoppers, 4 plants, and nitrogen. His field experiments mostly matched qualitative predictions of the Yodzis method (sign and significant or not), but not the magnitudes. Demonstrates that the method works but would be very difficult to apply accurately in complicated systems.

8. Island Biogeography

Theory: MacArthur & Wilson (1963) Species Equilibrium Model Predicts equilibrium abundance and equilibrium turn-over rates.

$$\frac{dS}{dt} = \underbrace{\lambda(P - S)}_{\text{colonization}} - \underbrace{\mu S}_{\text{extinction}} \tag{13}$$

See handout

Experimental tests

- Simberloff & Wilson (1969) Defaunate mangroves, observe return to same equilibrium number (but differing identity) of species, concave colonization rate, and the distant effect.
- Diamond (1969) Birds on Channel Islands over 51 years, showed equilibrium turn-over rates. Critiqued that incomplete sampling in one interval may look like a turnover that didn't actually occur, while sampling too infrequently increases chance a species appears and disappears without being counted.
- Spiller et al. (1998) spiders recover equilibrium species richness quickly, lizards slowly, due to different dispersal / colonization rates.