Competition: Observations and Experiments

Cedar Creek MN, copyright David Tilman
Resource-Ratio (R*) Theory

• Species differ in critical limiting concentration for resources (R* values)
• R* values differ among species as a result of resource allocation trade-offs
• Resource consumption vectors determine ratio of resource use
• When ZNPG isoclines cross over species potentially can coexist
Experimental test of $R^*$ using algae

**FIGURE 2.6.** (B) Top: Examples of zero-growth isoclines for $SiO_2$ and $PO_4$ for two algal species, Asterionella and Cyclotella. Within the shaded region each species can increase in population size. Note that the lowest $R^*$ for each species is for a different resource. Bottom: The outcome of competition between these species is described well by the isoclines and consumption vectors. Diamonds = Cyclotella wins; dots = stable coexistence; stars = Asterionella wins. (Adapted with permission from Tilman, D. Resource competition and community structure. © 1982 by Princeton University Press.)

Species coexist when each is limited by the resource for which it has the highest $R^*$ value.
Can R* promote multi-species coexistence?

Yes, but only if resource supply rates are variable in space. Different species coexist *at equilibrium* according to resource supply at particular locations.

Tilman (1988) Fig. 2.10a
Can $R^*$ promote multi-species coexistence?

Species differences in $R^*$ across gradients of resource availability.
How much evidence is there for R* Theory ‘in the wild’??

Miller et al. (2005) reviewed tests of R* theory:

1,333 citations of R* theory papers
26 tests of at least one R* prediction (42 tests total)
31 tests supported prediction (11 not)
37 of 42 tests in freshwater/marine systems

Only 5 studies with terrestrial plants --3 supported R*

ALL carried out at Cedar Creek, Minnesota by Tilman and collaborators

So, why are we calling this a theory?
Why so few tests?

Hard to measure $R^*$ values (hard to manipulate nutrients effectively and retain mycorrhizae, soil structure etc)

If you can do it, then it is expensive to replicate $R^*$ measurements for multiple species

Difficult to measure resource availability in the field at the scale of individual plants.

NSF doesn’t seem to be interested in funding tests of it!!
Variation in soil nutrient availability in the BCI forest, Panama

Nitrogen:

Phosphorus:
Multispecies coexistence if there is sufficient variation in resource ratios across the landscape

Landscape-level variation in resource ratios
No evidence that variance or mean nutrient concentrations is related to local species richness in BCI forest

Plot of number of species present in a 20 x 20 m plot versus variance in nutrient concentrations in the plot

Hubbell et al. unpubl.
Niches and competition

R* is an *equilibrium theory*
Species coexist through competition-driven niche differentiation.

**Fundamental niche:** Conditions under which a species persists in the absence of competitors

**Realized niche:** More restricted conditions for persistence in the presence of other species. Stresses competitive interactions

*(Resource utilization niche:* Somewhat quantifiable measure of similarity in resource use. e.g. Use to compare diet of consumers and predators (Pianka 1986))*
Harpole and Tilman (2007)

If species partition resources, then more limiting resources provides more ‘niche dimensions’ that species can partition and higher species richness is maintained.

Experiment and observational study in California grassland adding limiting resources: N, P, base cations and moisture in factorial experiment.

Adding resources increases productivity; effects on species composition may be transitory. Also looked at how multiple resources affect species richness (number of species) at Park Grass Experiment, Rothamstead UK (annual fertilizer additions for 150 yrs).
Declines also observed in factorial nutrient addition (a), and across range of plots that have observed differences in concentrations of resources (b).

Persistent declines in richness at Park Grass Experiment at Rothamstead (c).
MacArthur (1958)
How do multiple warbler species coexist?

5 warbler species (*Dendroica* spp.)
Mainly insectivorous. Similar size/shape bill structure
Strong diet overlap (differences in frequencies of prey types)
*Live together in relatively homogenous 15-20 m spruce forest*
Activity maps for individual species

Fig. 2. Cape May warbler feeding position. The zones of most concentrated activity are shaded until at least 50% of the activity is in the stippled zones.

Fig. 3. Myrtle warbler feeding position. The zones of most concentrated activity are shaded until at least 50% of the activity is in the stippled zones.
Competition among *Anolis* lizards

(Pacala and Roughgarden 1982)

How does resource partitioning influence strength of competition?

Compare 2 pairs of abundant insectivorous diurnal *Anolis* lizards on 2 Caribbean islands

(Anoles have their own blog at http://www.anoleannals.org)
Characterizing resource partitioning in *Anolis*

1. Body size. Strongly correlated with prey size in *Anolis*  
   **St Maarten** anoles: *complete overlap* in body size  
   **St Eustatius** anoles: partial overlap in body size

2. Foraging location.  
   **St Maarten** anoles: *complete overlap* in perch height  
   **St Eustatius** anoles: no overlap in perch height

**Experiment:**  
Replicated enclosures on both islands  
Enclosures stocked with one or both species (with *A. wattsi*)

Response variables: Effect of local *A. wattsi* sub-species on  
perch height and growth rate of *A. gingivinus* and *A. bimaculatus*
St Maarten

A. gingivinus

A. wattsii pogus

Overlap in perch height and body size
St Eustatius

A. bimaculatized

A. wattsi schwartzi

No overlap in body size or perch height
Results:

St Maarten Anole (similar resource use – anoles overlap)
- Growth rates of *A. gingivinus* in presence of *A. wattsi* half of *A. gingivinus* alone
- Perch height of *A. gingivinus* doubled from 0.44 m to 0.88 m in presence of *A. wattsi*

St Eustatius Anole (different resource use)
No effect of presence of *A. wattsi* on growth or perch height of *A. bimaculatis*

Why is St Maarten, with strong present-day interspecific competition between two species adjacent to St Eustatius, an island with weak present-day interspecific competition???
Adaptive radiations of *Anolis* lizards (Losos et al. 1998)

Looked at lizard community assemblages on Greater Antillean Islands (Cuba, Jamaica, Hispaniola, Puerto Rico)

Define six ‘ecomorphs’ of *Anolis* based on morphometric characters associated with habitat use (size, shape of anoles that influence where they live/forage).

Most ecomorphs occur on each island

How would you predict that members of the same ecomorphs present on different islands are related? – 2 options…

Anolis in the same ecomorph category are not closely related. Only two cases where a single ecomorph has evolved twice on the same island.

Interpretation: Interspecific competition drives ecomorph differentiation (limiting similarity)
Character displacement

*Or the Ghost of competition past...*

A distribution pattern where sister species are recognizably different in zones of overlap (sympatric) but virtually indistinguishable where each occurs alone.

Character displacement results from interspecific competition in the zone of overlap (Schluter 1994) forcing species to partition resources.
**Hypothesis:** If differences in resource use among anoles is a consequence of historical competitive interactions

**Predict:**
St Maarten anoles came together recently - intense competition

St Eustatius anoles been around a long time - past competition has led to character displacement

**Evidence:**

Pacala and Roughgarden (1985) no evidence for this hypothesis! Use biogeographic history of Caribbean basin and electrophoretic evidence to argue that St Maarten anoles represent an old co-evolved community of competing species
Character displacement in the Small Indian Mongoose

Simberloff et al. (2000)

*Herpestes javanicus*

Native range:
Iraq to the Malay peninsula

Populations are sympatric with two larger species *H. edwardsii* & *H. smithii* but only in part of the native range

Mongooses introduced for rat control from India to Jamaica in 1872 (9 individuals), thence across the Caribbean, on to Hawaii in 1883. Independent introductions to Mauritius (1900), Fiji (1883), Okinawa (1910) among others...
Hypothesis: *Mongoose size is an adaptation to competition from congeners (= species in the same genus)*

Two predictions:
*In its native range, in areas where larger congeners are missing, the Indian Mongoose will be larger.*
*In its introduced range, in the absence of its two larger congeners the Indian Mongoose will increase in size.*

Dependent variables:
Skull length and diameter of the upper canine tooth (killing tooth)
Fig. 2. Maximum diameter (mm) of upper canine ($C_{supL}$) and sexual size dimorphism (SSD) for this trait for *Herpestes javanicus* in its native and introduced range. For $C_{supL}$, symbols on the left represent mean female size; symbols on the right represent mean male size.
Schluter and McPhail (1992) survey literature on character displacement and list criteria necessary to exclude other potential explanations:

- Pattern should not arise by chance (appropriate statistical model)
- Phenotypic differences should have a genetic basis
- Differences should arise evolutionarily not by selective survival of different sized invaders.
- Similar phenotypes should actually compete for resources.
- Morphological differences should reflect differences in resource competition (food use here).
- Sites of sympatry (species overlap) and allopatry (non overlap) should not differ in food or other environmental features in a way that would account for the pattern.
Competition trade-offs

Diversity could be maintained if species *partition* resources (R*, warblers, mongooses) or if differences in competitive ability trade-off with other abilities.

Many examples exist of competition-dispersal or competition-colonization trade-offs (*Daphnia*, insects, fungi, plants)

Traits that confer high competitive ability come at a cost – associated with speed of development, dispersal ability, persistence.
Example of a colonization-competition trade-off:
Neotropical *Drosophila* species (Sevenster and Van Alphen 1993; Krijger et al. 2001)

Diverse assemblages of *Drosophila* species coexist on decaying fruits in tropical forests (feeding on yeasts).

*Species differ markedly in larval development time*

**Experiment:** Pairwise competition trials between 7 species varying in development times.

**Result:** Species with long development times suffered greater interspecific competition, but had greater survival times (potentially an advantage in finding new food resources).
Fig. 1. The starvation time of adults (experiment B5) versus developmental period (experiment B1) for 18 species. Circles indicate means, bars their standard errors. $\tau$ is Kendall's rank correlation on the means. Line fitted by linear regression (see Table 7). The inset shows the results of the independent comparisons method, which removes the effect of phylogenetic dependence. The data points in the inset represent nodes in the phylogenetic tree and show the differences in developmental period and starvation time between branches of the node.
Speed of development is traded off with various factors:

- *Resistance against abiotic stresses* (e.g. dessication, temperature extremes) increases with development time

- *Adult survival*. A long adult life improves the probability of colonizing a new breeding site (decaying fruit) in time and space

- If resource availability fluctuates through the year, or if flies are specialized on different fruit types with different abundances then variation in development time can maintain species diversity.
Testing mechanistic models for resource partitioning is difficult!

Observational studies are (mostly) consistent with the hypothesis that coexistence is linked to resource heterogeneity.

Some evidence also supports limits to the similarity of coexisting species.

Challenges to a competition-centric view of community assembly comes from species-rich communities where the number of coexisting species far exceeds the number of limiting resources.