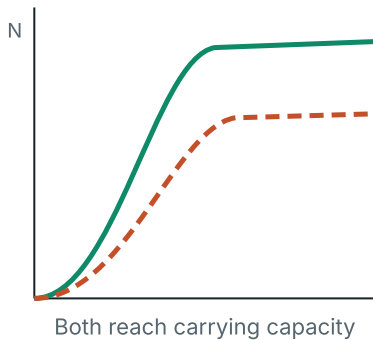


Gause's Law

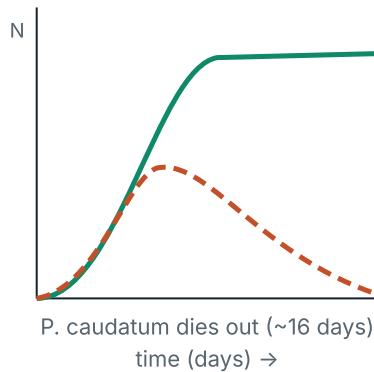
The competitive exclusion principle (G. F. Gause, *The Struggle for Existence*, 1934)

Statement. Two species competing for exactly the same limiting resources cannot coexist indefinitely. The slightly more efficient competitor eventually eliminates the other. "*Complete competitors cannot coexist.*"

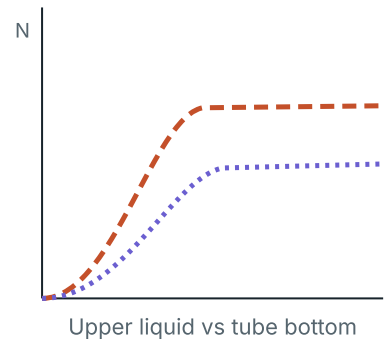
1 · Grown separately



2 · Grown together



3 · Different niches



— P. aurelia

- - - P. caudatum

..... P. bursaria

Schematic of Gause's *Paramecium* cultures. N = population density. Shapes follow the published results; values are not to scale.

EXPERIMENT 1

Grown separately

P. aurelia and *P. caudatum* each show logistic (S-shaped) growth and level off at their own carrying capacity K.

EXPERIMENT 2

Grown together

On the same bacterial food, *P. aurelia* grows faster and uses food more efficiently. *P. caudatum* declines to local extinction.

EXPERIMENT 3

Niche separation

P. caudatum feeds on bacteria in the upper liquid; *P. bursaria* feeds at the bottom on yeast. Both persist, each at lower density.

Conditions for exclusion

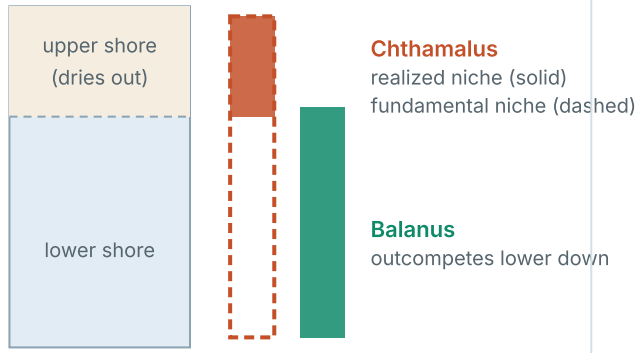
- Same single limiting resource (food, space, nutrient)
- Stable, uniform environment with no refuges
- No niche shift is possible
- No predation, disturbance or immigration resetting the contest

Key terms

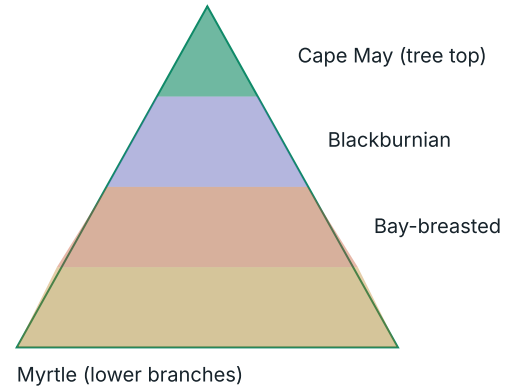
- **Niche:** a species' full role and resource use
- **Fundamental niche:** range possible without competitors
- **Realized niche:** range actually used with competitors
- **Resource partitioning:** dividing a shared resource so species can coexist

How species escape exclusion

Connell's barnacles (1961)



MacArthur's warblers (1958)



Left: *Chthamalus* could live lower on the shore (fundamental niche) but is restricted to the upper zone by competition from *Balanus* (realized niche). Right: warbler species feed in the same spruce trees but in different zones (simplified).

Mechanisms of coexistence

- **Spatial partitioning:** different zones (warblers, barnacles)
- **Temporal partitioning:** different feeding times, e.g. hawks by day, owls by night
- **Dietary partitioning:** different prey sizes or food types
- **Character displacement:** traits diverge where species overlap, e.g. beak depth in Darwin's finches
- **Disturbance and predation:** keep the dominant competitor below K (Paine's starfish experiment)

Mathematical basis: Lotka–Volterra competition

$$dN_1/dt = r_1 N_1 (K_1 - N_1 - \alpha_{12} N_2) / K_1$$

$$dN_2/dt = r_2 N_2 (K_2 - N_2 - \alpha_{21} N_1) / K_2$$

α_{12} = effect of species 2 on species 1. Stable coexistence only when $\alpha_{12} < K_1/K_2$ and $\alpha_{21} < K_2/K_1$, i.e. each species limits itself more than its rival. Otherwise one species is excluded.

Possible outcomes of the Lotka–Volterra model

CONDITION	OUTCOME
$K_1 > K_2/\alpha_{21}$ and $K_2 < K_1/\alpha_{12}$	Species 1 always wins
$K_2 > K_1/\alpha_{12}$ and $K_1 < K_2/\alpha_{21}$	Species 2 always wins
$K_1 > K_2/\alpha_{21}$ and $K_2 > K_1/\alpha_{12}$	Unstable: winner depends on starting numbers
$K_1 < K_2/\alpha_{21}$ and $K_2 < K_1/\alpha_{12}$	Stable coexistence

Limitations and criticisms

- **Paradox of the plankton** (Hutchinson, 1961): many phytoplankton share a few nutrients yet coexist, because conditions change before exclusion is complete.
- Hard to falsify: if species coexist, one can always claim their niches differ.
- Real environments are patchy, seasonal and disturbed.

Significance

- Foundation of niche theory (Grinnell, Elton, Hutchinson)
- Explains community structure and species packing
- Explains why invasive species can displace natives (e.g. grey squirrel replacing red squirrel in Britain)
- Basis of resource-partitioning and character-displacement studies

Exam one-liner. "Complete competitors cannot coexist; one will eliminate the other unless their niches differ" (Gause, 1934). Also called the competitive exclusion principle or Grinnell's axiom. Proof: *Paramecium aurelia* excluded *P. caudatum* in mixed culture.