Teórica 5:
Interacciones interespecíficas:

Competencia

Repaso Teórica 4: Dinámica poblacional

- ¿Qué es el crecimiento exponencial?
- ¿Cómo agregamos densodependencia?
- ¿Se llega siempre a un punto de equilibrio estable?
- ¿Cómo varía la tasa de crecimiento de la población y per cápita en cada modelo?
- ¿Cómo podemos modificar el modelo logístico original?
- ¿Qué nos dice la evidencia experimental y de campo sobre la dinámica poblacional?
- ¿Cómo podemos estudiar la dinámica de poblaciones con estructura de edades y tamaños?

Teórica 5: Esquema conceptual

- Algunos ejemplos
- Definición de competencia
- Modelos matemáticos de competencia
- Evidencia: experimentos de laboratorio y de campo
- Evolución de la habilidad competitiva

Distribución de aves del archipiélago Bismarck

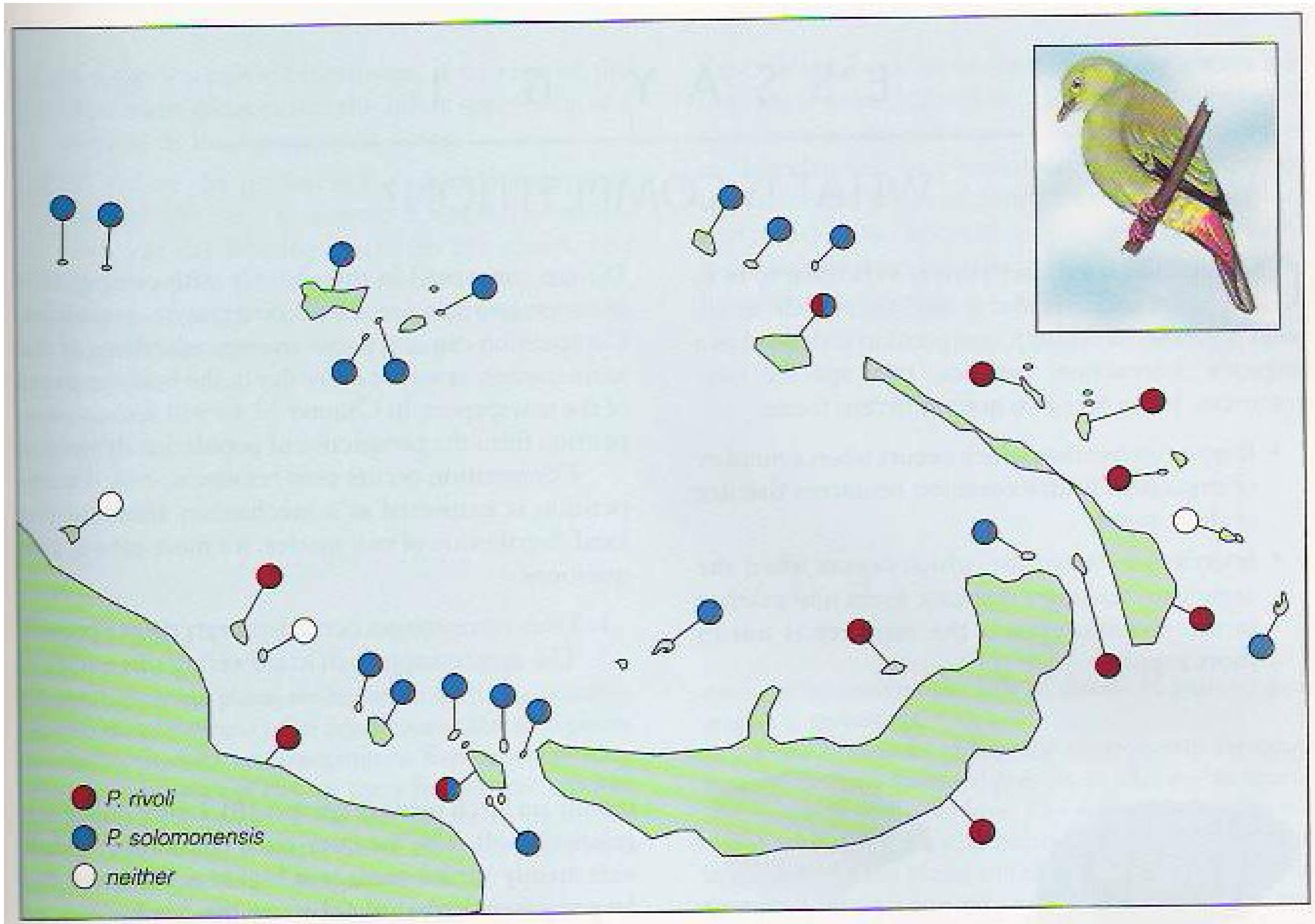
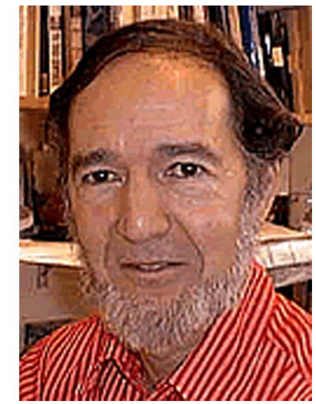


FIGURE 6.9
Checkerboard distribution of two closely related species of fruit pigeons in the Bismarck Archipelago of the western Pacific Ocean off New Guinea. Note that either Ptilinopus pivoli *(R) or* P. solomonensis *(S) occurs on most of these islands, and only one or two islands have both. (From Diamond 1975.)*



Jared
Diamond

Dieta del guanaco y del ganado en La Payunia

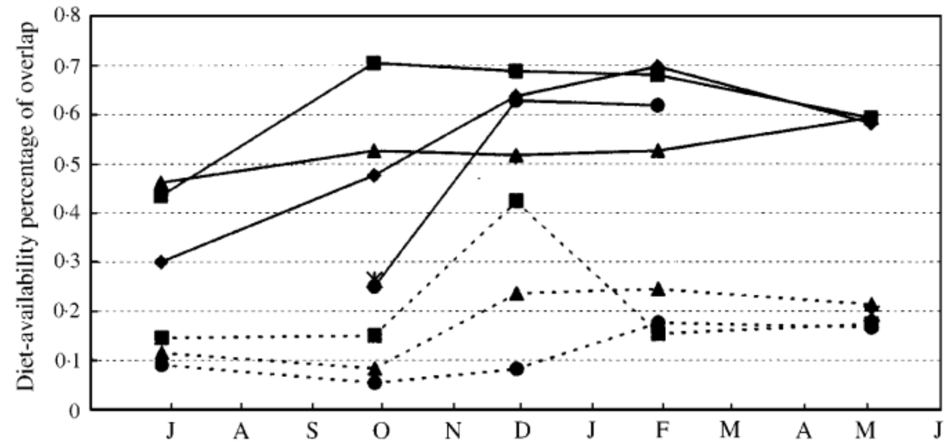


Figure 4. Similarity during the year between the diet of each ungulate and plant availability in sandy and rocky habitats (continuous and dash lines, respectively) —◆— Guanaco; —■— Cattle; —▲— Horses; —●— Sheep; —✳— Goats.

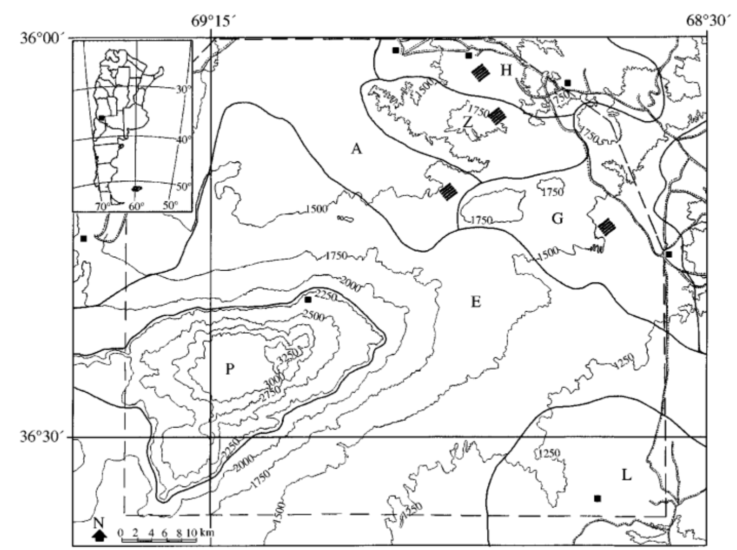


Figure 1. Location of habitat types (H: Huayquerías coloradas, Z: Zaino, G: Guadalosos, A: Aparejo, E: Escoriales, P: Payunes, L: Lonco Vaca), limits among habitats (——), sampling areas (▨) and 'puestos' (■) in La Payunia Reserve (Mendoza, Argentina).

Fuente: Puig et al. (2001) J. Arid Env. 47: 291-308

Dieta del guanaco y del ganado en La Payunia

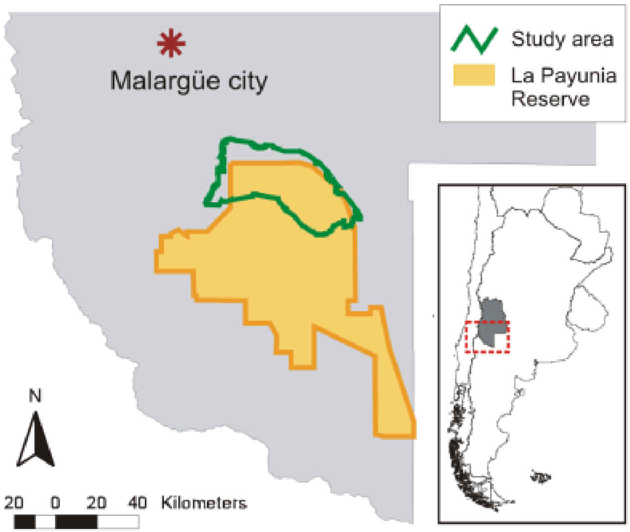
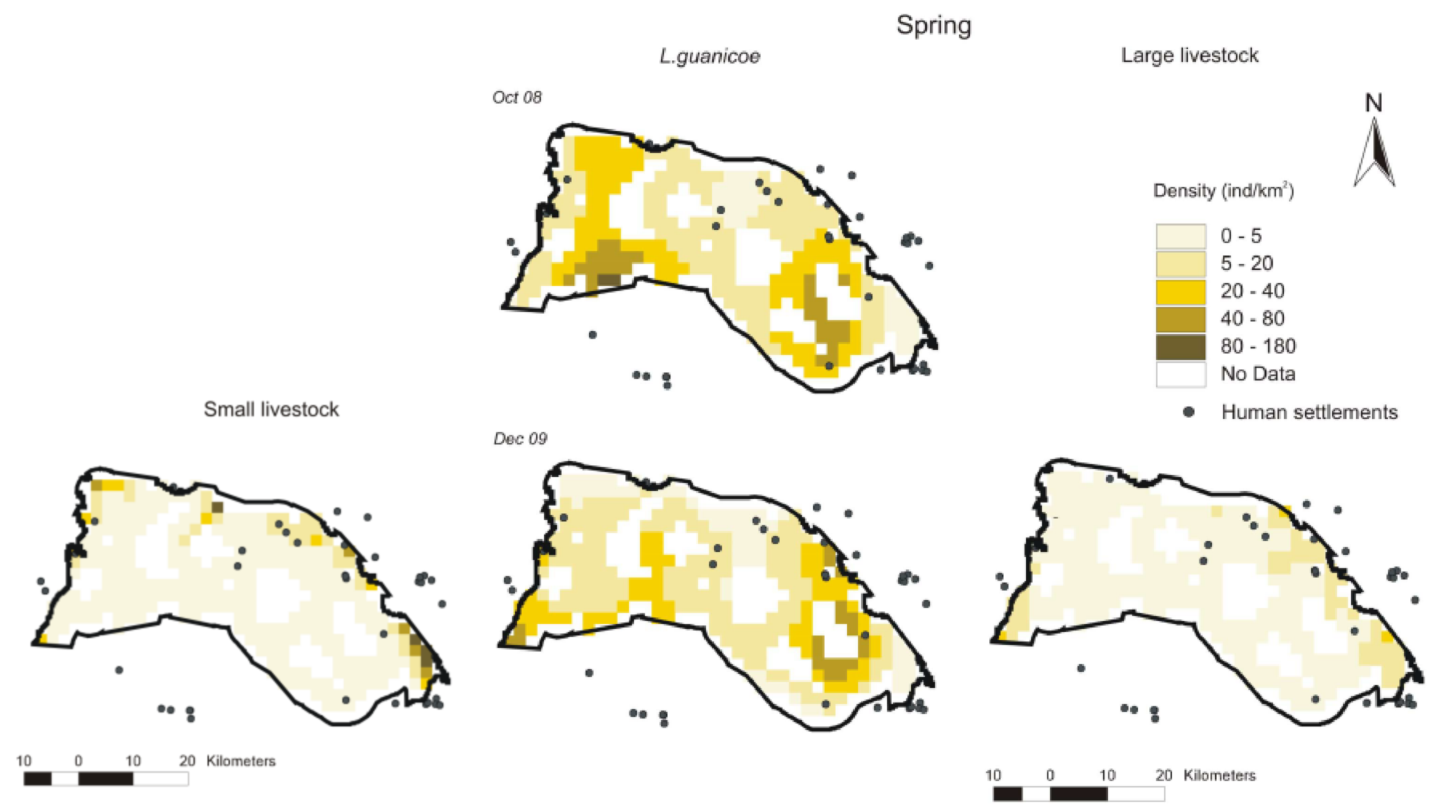


Figure 1. Study area in the northern part of La Payunia Reserve and surrounding area. It is located in Mendoza province, central-west Argentina.
doi:10.1371/journal.pone.0085960.g001



Fuente: Schroeder et al. (2014) PLoS ONE 9: e85960

Abundancia de hormigas nativas y avispas exóticas en cebos

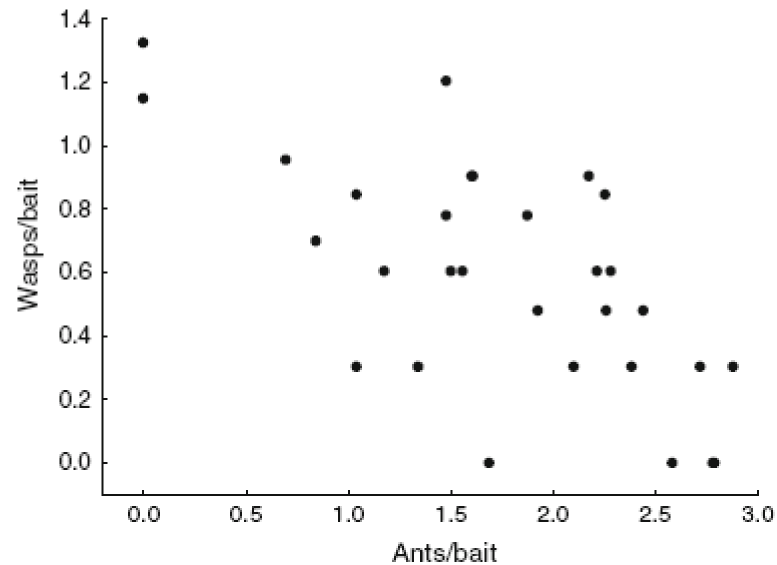


Fig. 3 Relationship between the number of wasps and ants per bait in control treatments. Each point represents a food bait. Data were transformed as $x' = \log(1 + x)$

Fuente: Masciocchi et al. 2010. Biological Invasions 12: 625-631

¿Compiten estas especies por los recursos o el espacio?
¿Pueden coexistir?

Tipos de interacciones interespecíficas

Especie 1

Especie 2

	+	-
+	Mutualismo	Depredación Herbivoría Parasitismo
-	Depredación Herbivoría Parasitismo	Competencia
0	Comensalismo	Amensalismo

Tipos de competencia

- Competencia por recursos: dos organismos utilizan recursos comunes que son escasos.
- Competencia por interferencia: dos organismos que buscan un recurso se dañan mutuamente en el proceso, aun cuando los recursos no son limitados.

Modelo de Lotka-Volterra

Alfred Lotka (1880-1949)

Vito Volterra (1860-1940)

Modelo de Lotka-Volterra

Ecuaciones logísticas para poblaciones que no compiten

$$\frac{dN_1}{dt} = r_1(1 - \frac{N_1}{K_1})N_1$$

$$\frac{dN_2}{dt} = r_2(1 - \frac{N_2}{K_2})N_2$$

Modelo de Lotka-Volterra

Ecuaciones logísticas para poblaciones que compiten

Número equivalente de individuos de la especie 1

$$\frac{dN_1}{dt} = r_1(1 - \frac{N_1 + \alpha N_2}{K_1})N_1$$

Número equivalente de individuos de la especie 2

$$\frac{dN_2}{dt} = r_2(1 - \frac{N_2 + \beta N_1}{K_2})N_2$$

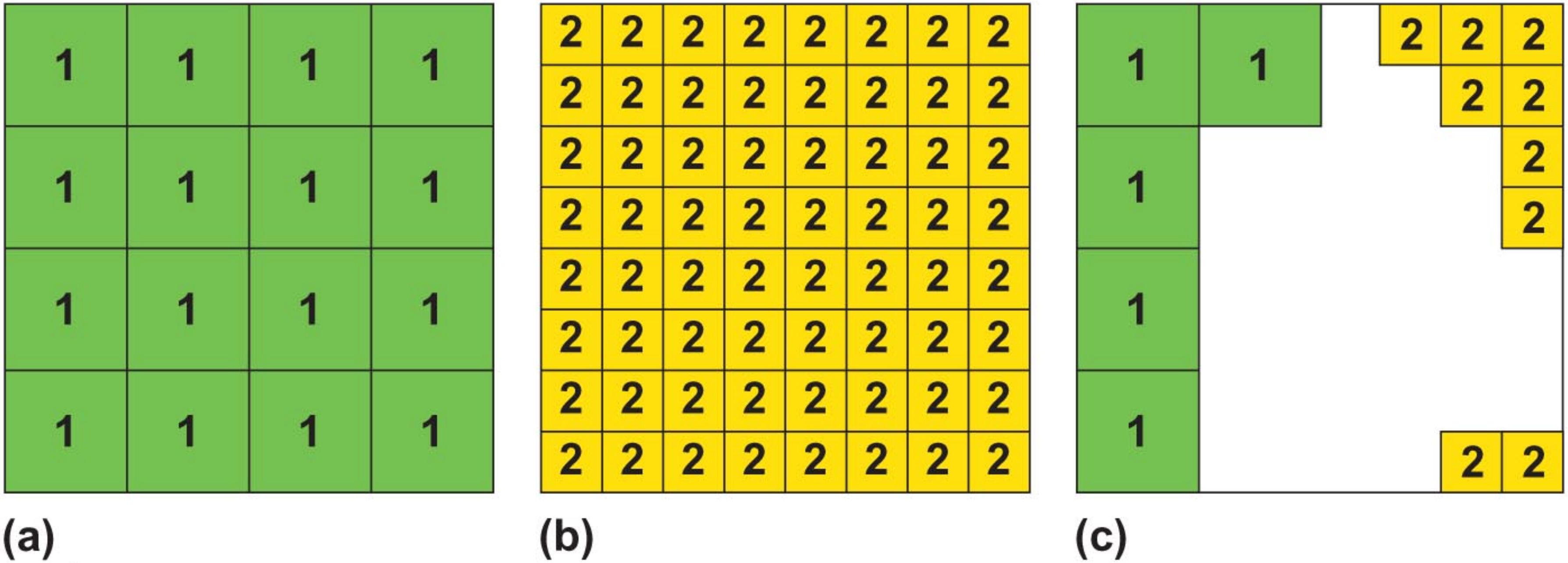
Modelo de Lotka-Volterra

$$\frac{dN_1}{dt} = r_1(1 - \frac{N_1 + \alpha N_2}{K_1})N_1$$

$\alpha = 0.25$

$\beta = 4$

$$\frac{dN_2}{dt} = r_2(1 - \frac{N_2 + \beta N_1}{K_2})N_2$$



Modelo de Lotka-Volterra

$$\frac{dN_1}{dt} = r_1(1 - \frac{N_1 + \alpha N_2}{K_1})N_1$$

$$\frac{dN_2}{dt} = r_2(1 - \frac{N_2 + \beta N_1}{K_2})N_2$$

¿Cuándo pueden coexistir N_1 y N_2?

Modelo de Lotka-Volterra: Equilibrio de la especie 1

$$\frac{dN_1}{dt} = r_1\left(1 - \frac{N_1 + \alpha N_2}{K_1}\right)N_1 = 0$$

o reordenando

$$\frac{dN_1}{dt} = r_1\left(\frac{K_1 - N_1 - \alpha N_2}{K_1}\right)N_1 = 0$$

Y esto es cero cuando

$$K_1 - N_1 - \alpha N_2 = 0$$

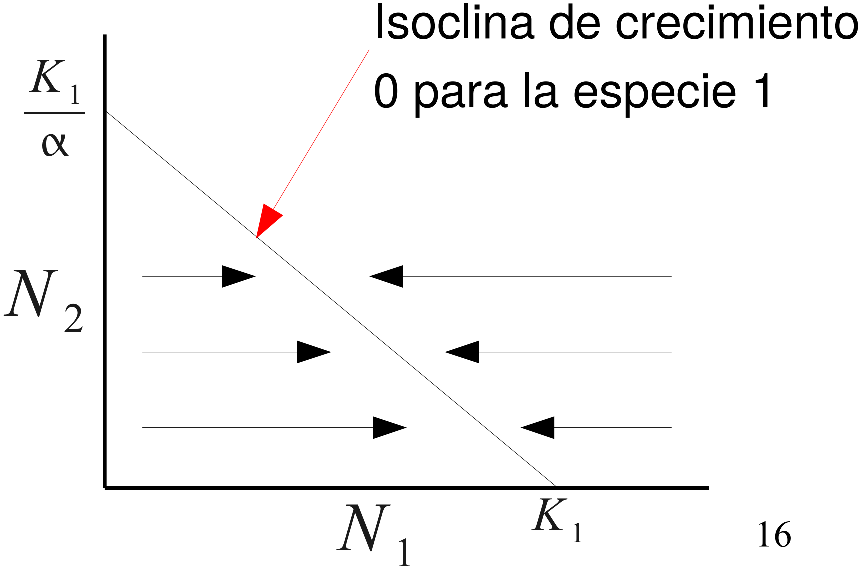
$$N_1 = 0$$

Entonces, si $N_2 = 0$

$$N_1 = K_1$$

Y si $N_1 = 0$

$$N_2 = \frac{K_1}{\alpha}$$



Modelo de Lotka-Volterra: Equilibrio de la especie 2

$$\frac{dN_2}{dt}=r_2\left(1-\frac{N_2+\beta N_1}{K_2}\right)N_2=0$$

o reordenando

$$\frac{dN_2}{dt}=r_2\left(\frac{K_2-N_2-\beta N_1}{K_2}\right)N_2=0$$

Y esto es cero cuando

$$K_2-N_2-\beta N_1=0$$

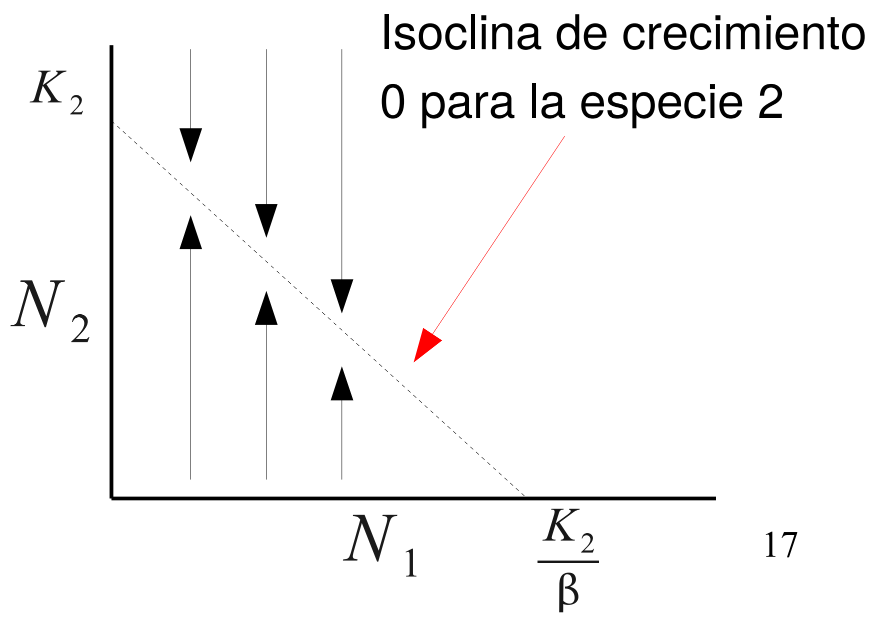
$$N_2=0$$

Entonces, si $N_1 = 0$

$$N_2=K_2$$

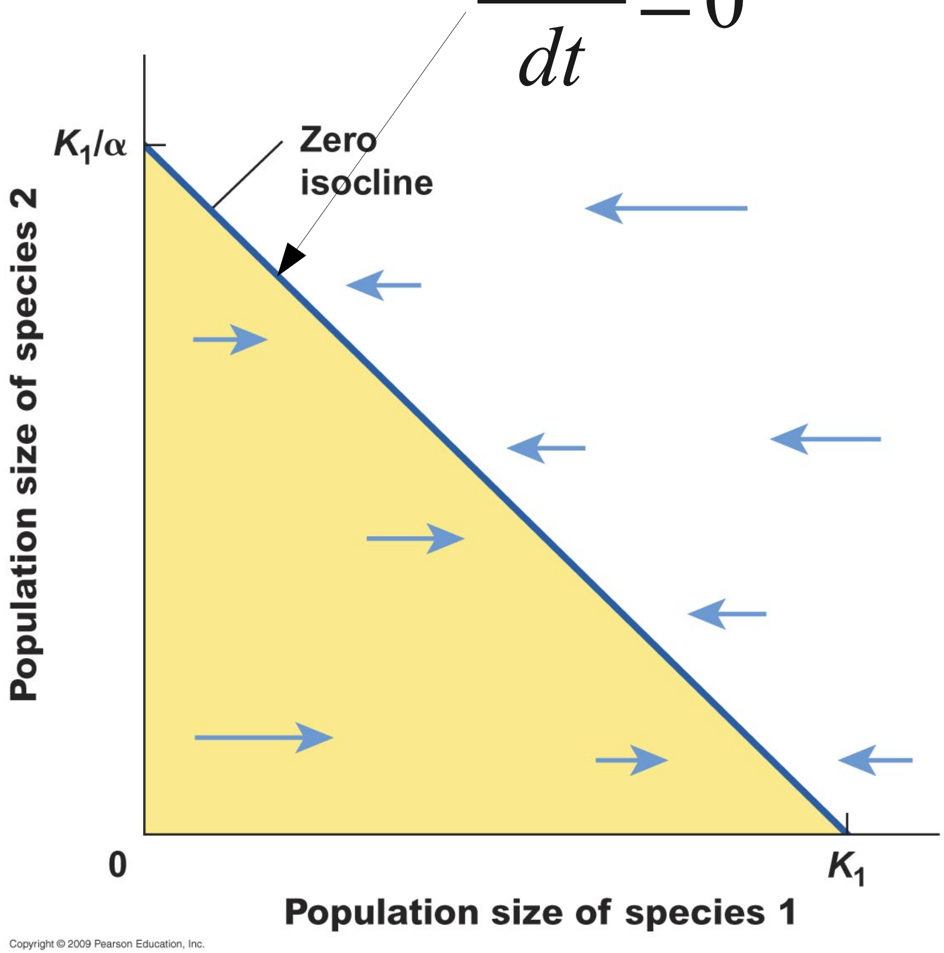
Y si $N_2 = 0$

$$N_1=\frac{K_2}{\beta}$$

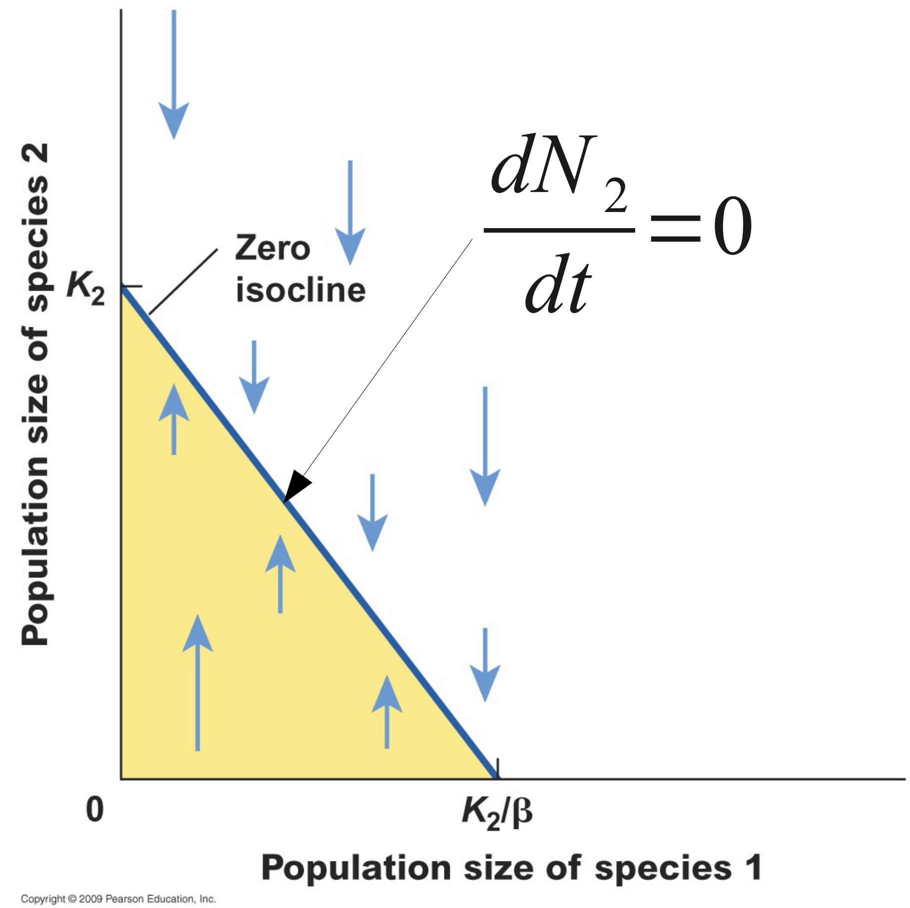


Modelo de Lotka-Volterra

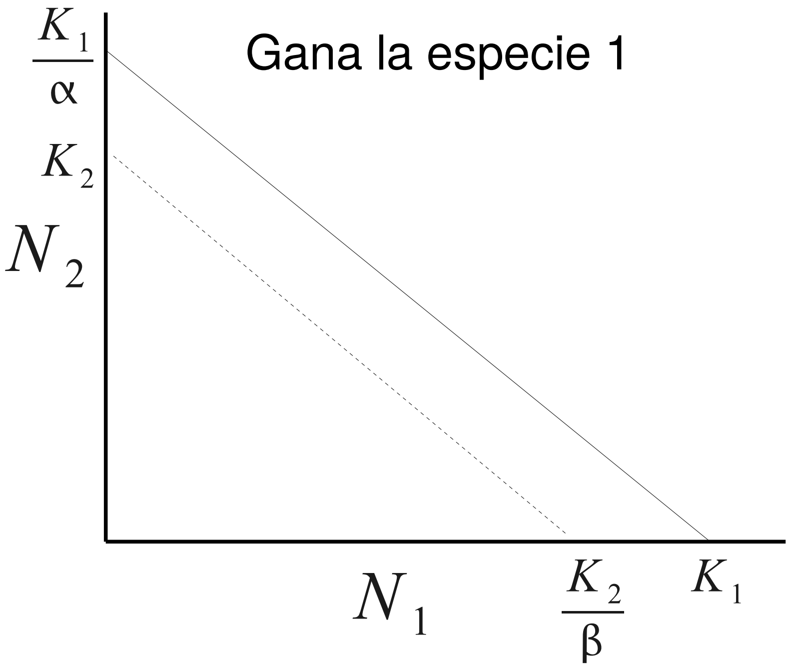
$$\frac{dN_1}{dt} = 0$$

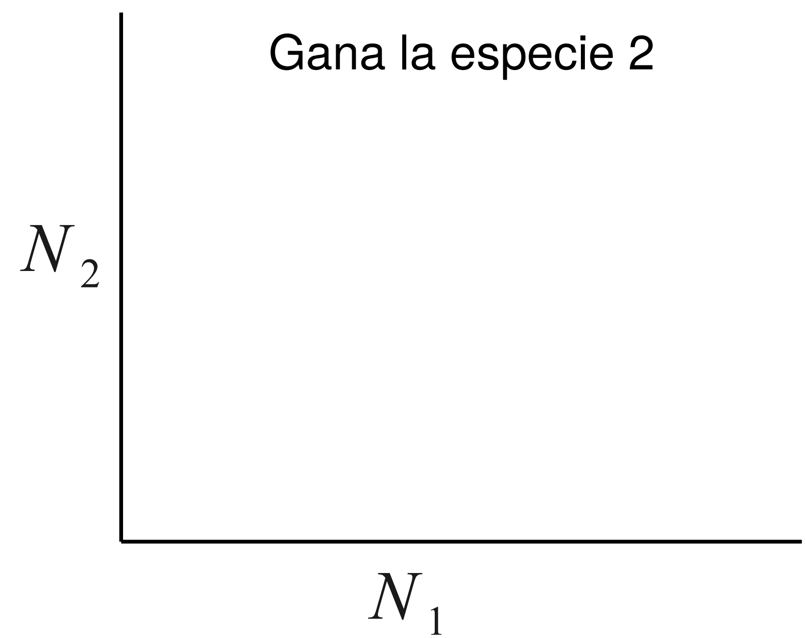


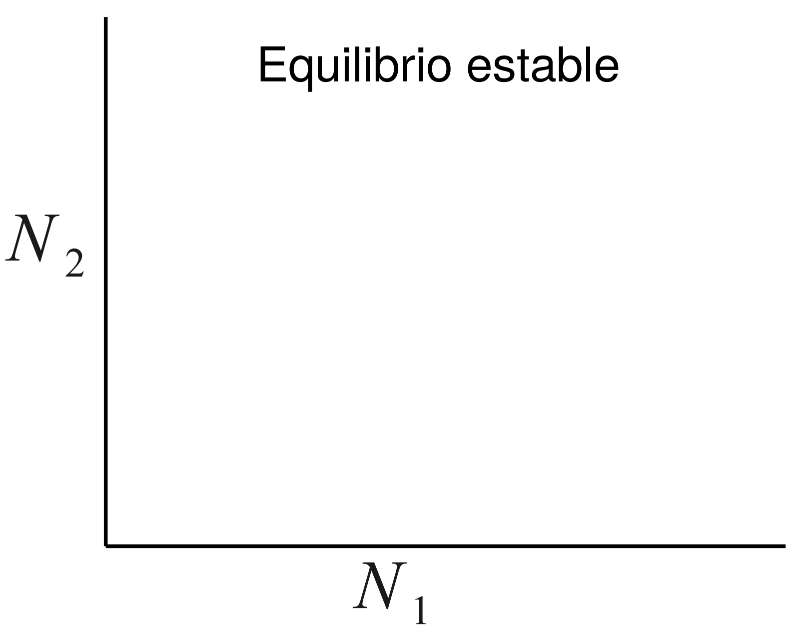
$$\frac{dN_2}{dt} = 0$$

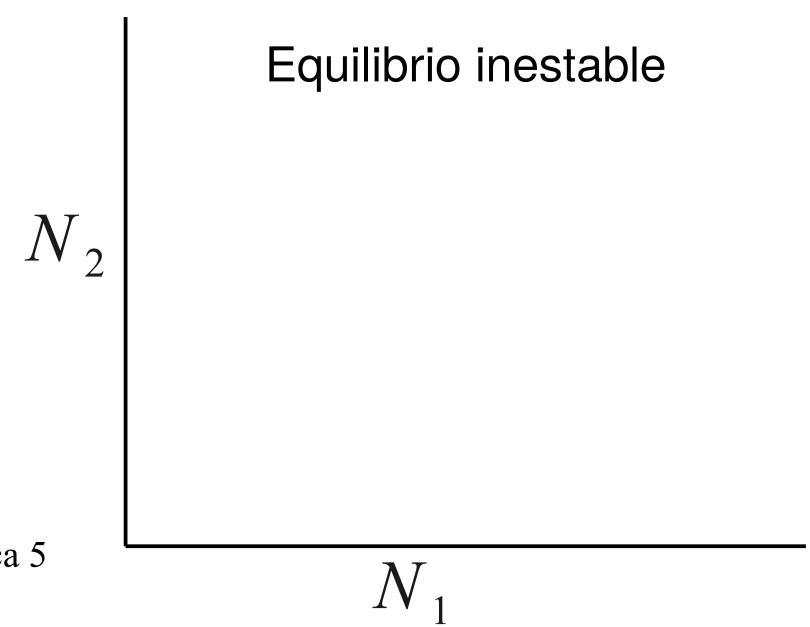


Modelo de Lotka-Volterra







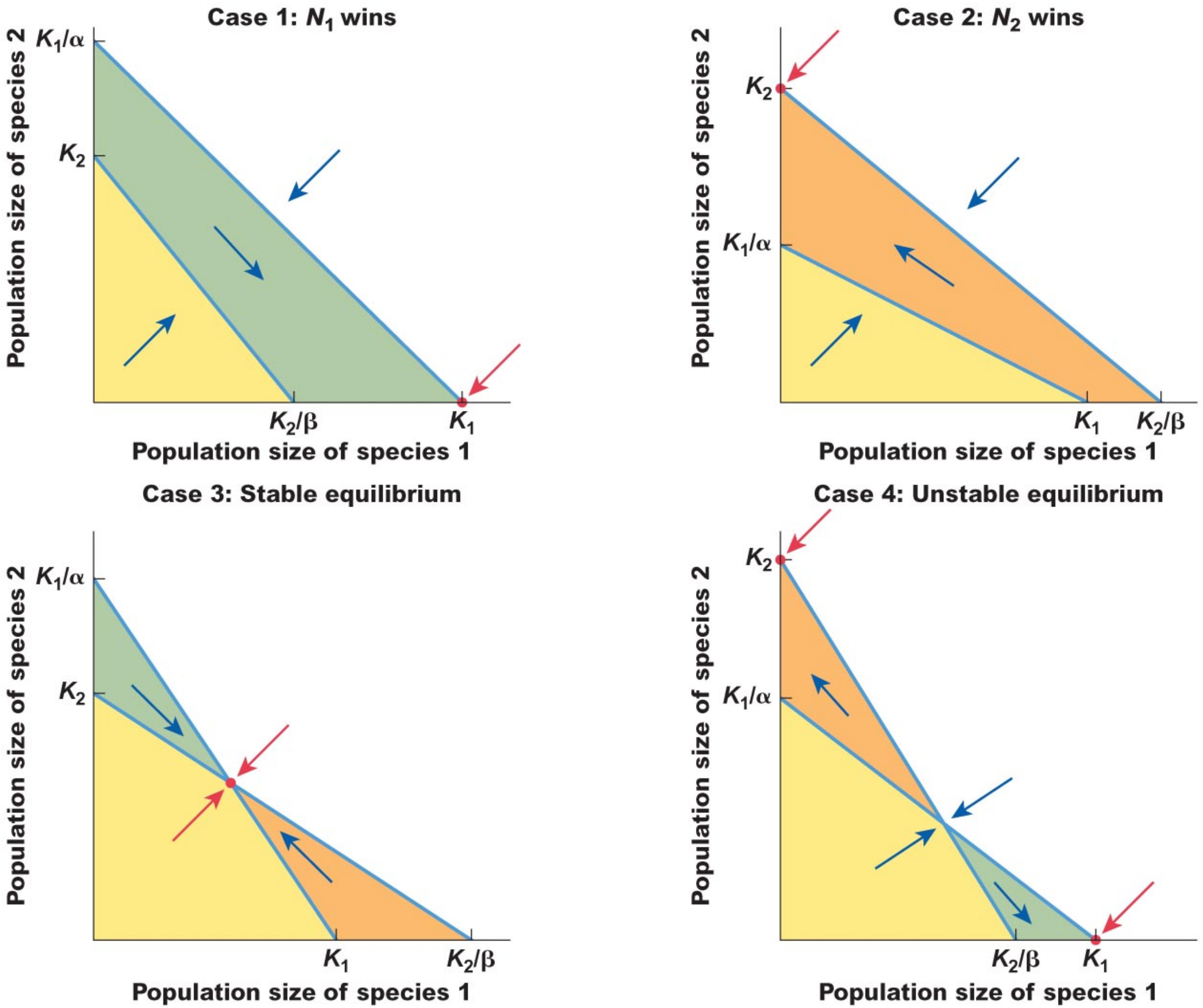


Modelo de Lotka-Volterra

Para la coexistencia estable, la competencia **intra**específica debe ser más fuerte que la **inter**específica para ambas especies, es decir:

$K1 < K2/\beta$

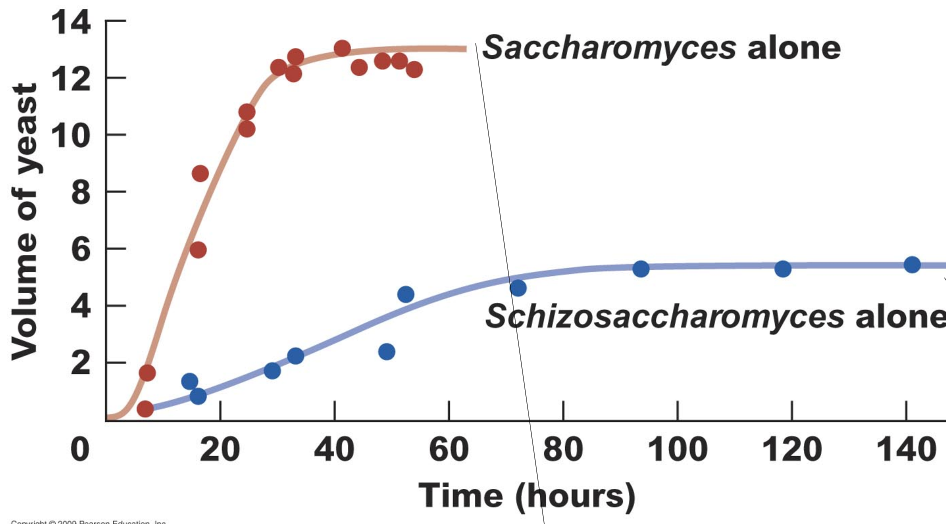
$K2 < K1/\alpha$

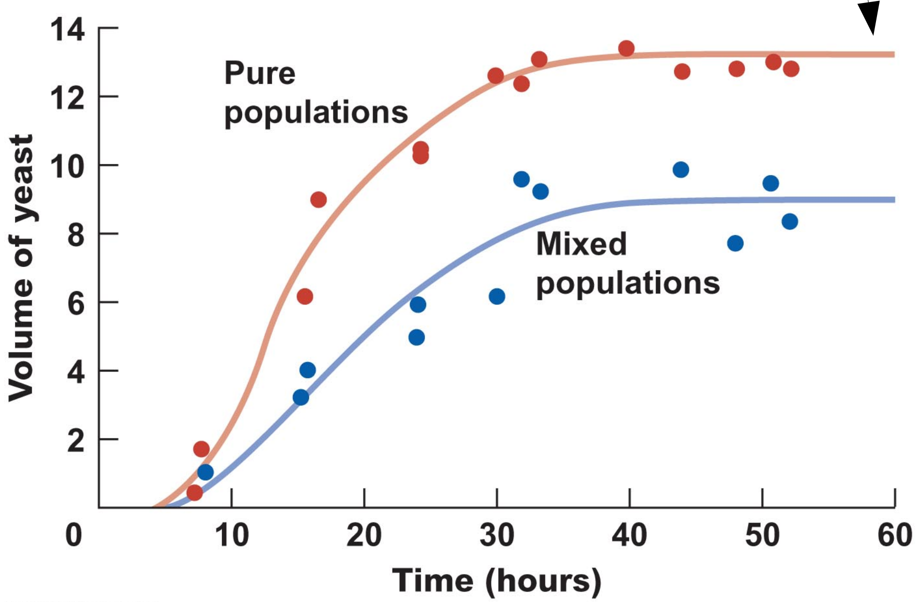


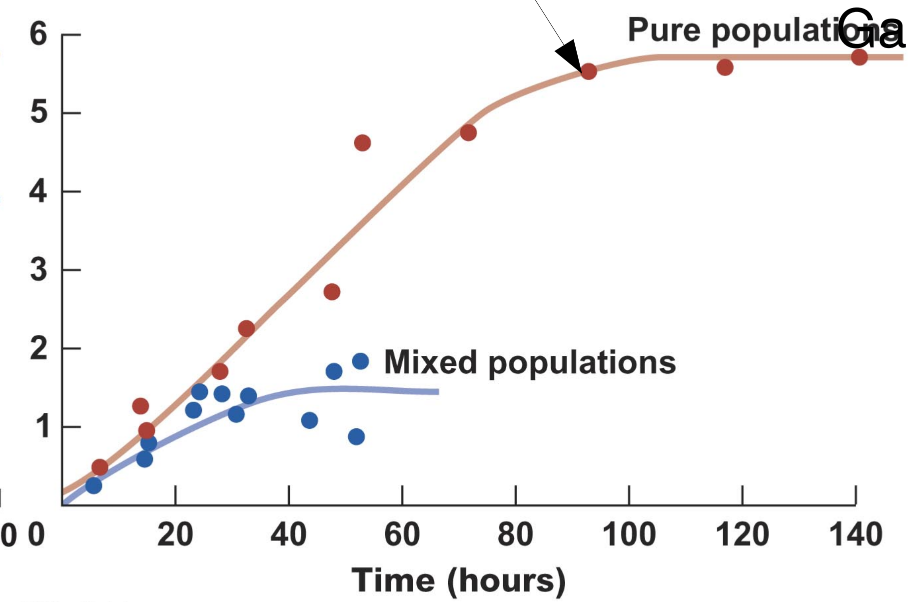
Condiciones para la coexistencia

- Coexistencia estable: $$\alpha < \frac{K_1}{K_2} < \frac{1}{\beta}$$
- Coexistencia inestable: $$\alpha > \frac{K_1}{K_2} > \frac{1}{\beta}$$
- Gana especie 1: $$\alpha < \frac{K_1}{K_2} > \frac{1}{\beta}$$
- Gana especie 2: $$\alpha > \frac{K_1}{K_2} < \frac{1}{\beta}$$

Experimento de Gause (1932)







Georgy Gause

Experimento de Gause (1932)

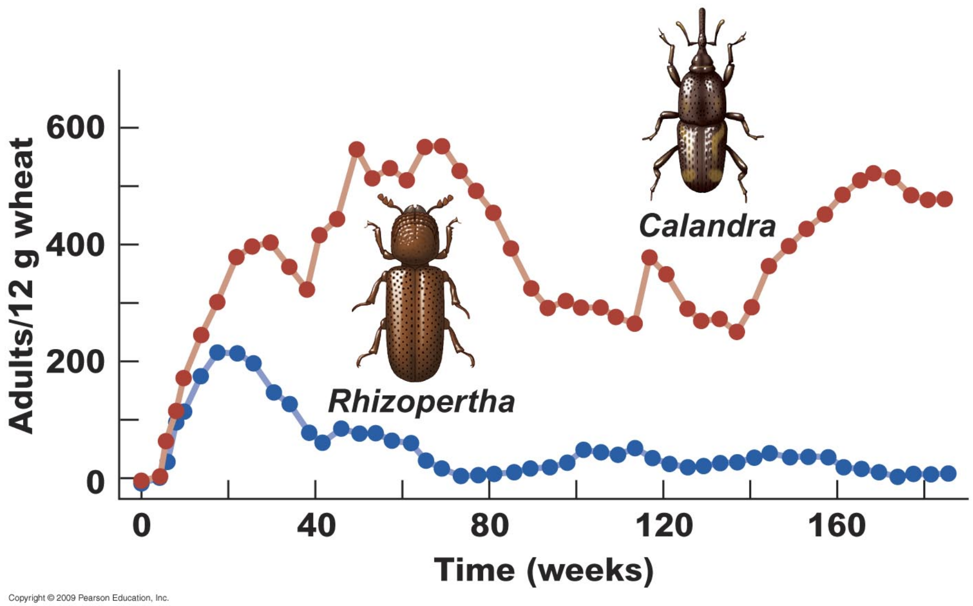
	Saccharomyces	**Schizosaccharomyces**
K	13.00	5.80
r	0.22	0.06

Age of Culture (hr)	*Competition coefficients* α *Saccharomyces*	β *Schizosaccharomyces*
20	4.79	0.501
30	2.81	0.349
40	1.85	0.467
Mean value	3.15	0.439

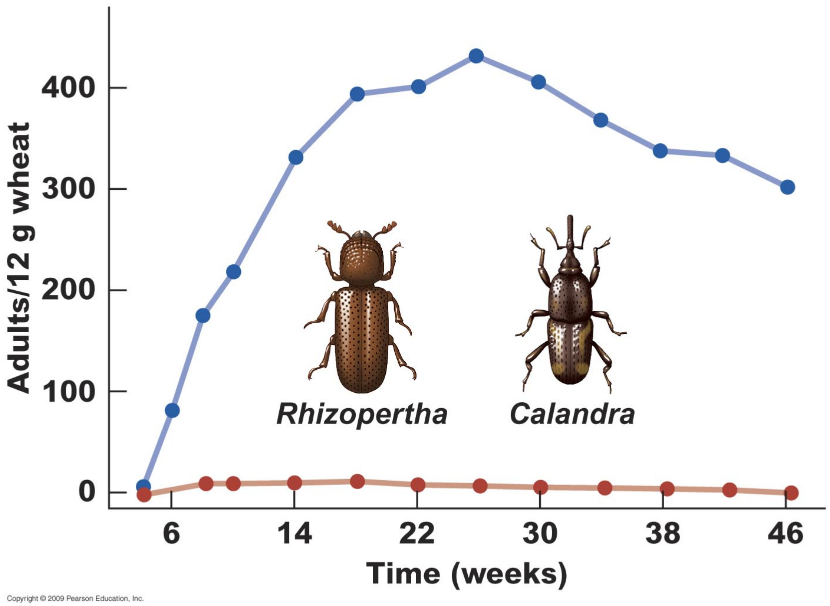
	Alcohol production (% EtOH/mL yeast)
Saccharomyces	0.113
Schizosaccharomyces	0.247

Experimento de Birch (1953)

Temperatura: 29.1 °C



Temperatura: 32.3 °C



Principio de Gause de la exclusión competitiva

Como resultado de la competencia, dos especies ecológicamente similares no ocuparán nichos similares, sino que se desplazan mutuamente de un modo tal que cada una tome posesión de ciertos tipos de recursos y formas de vida en las que tiene una ventaja sobre su competidor.

El concepto de nicho

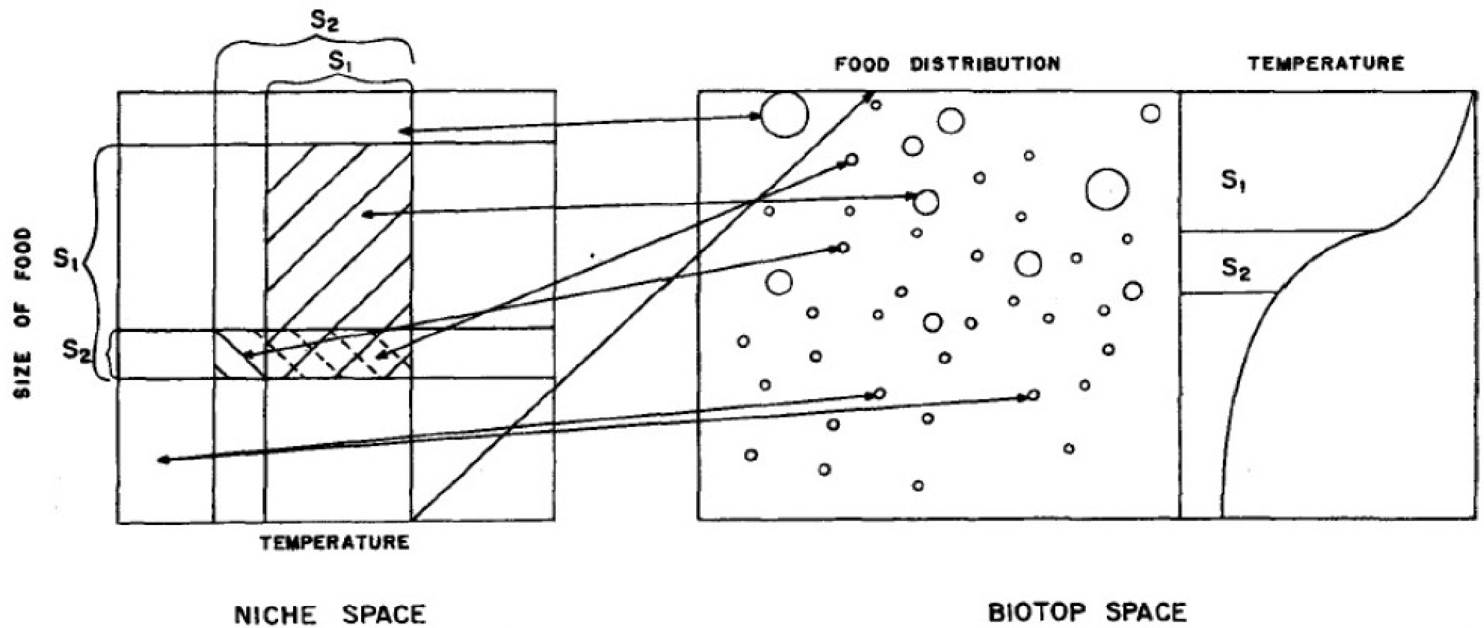
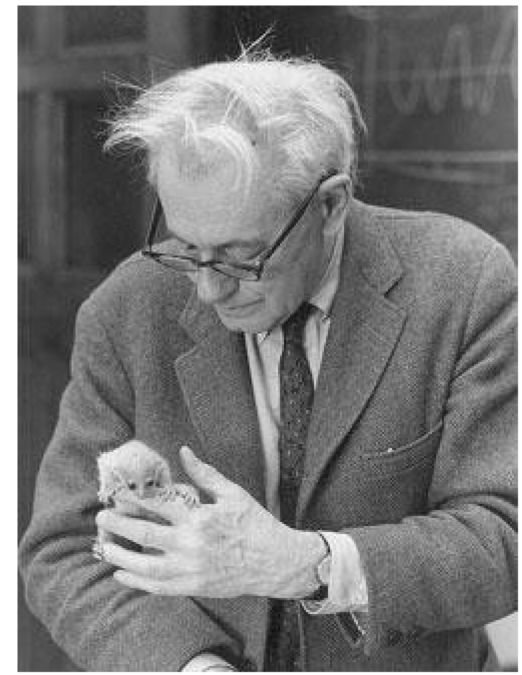


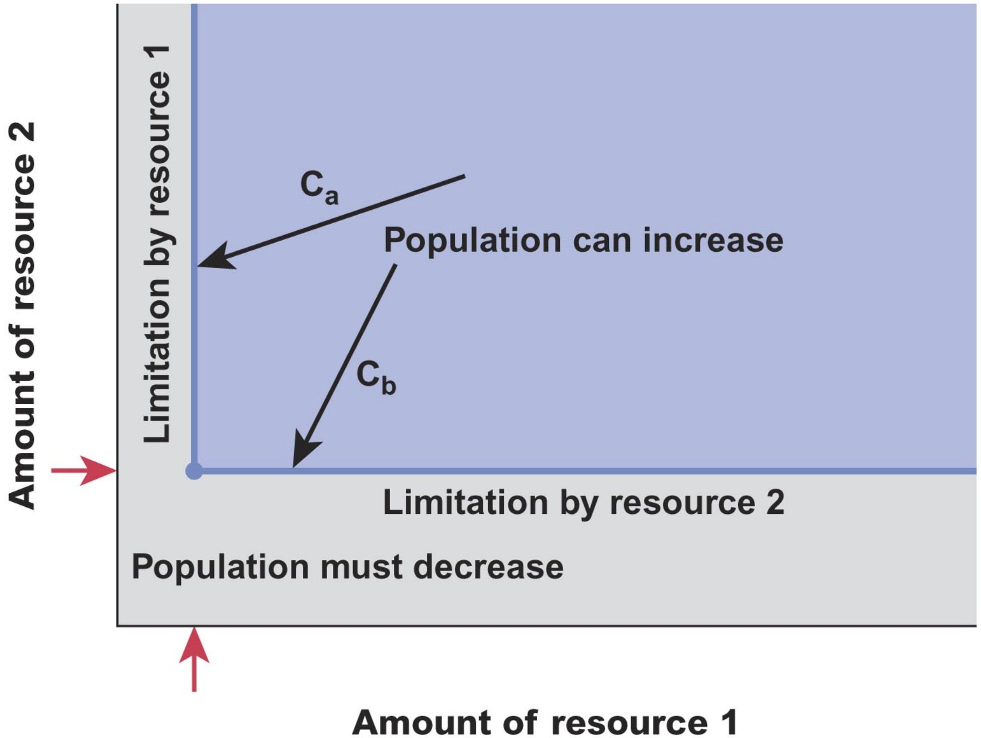
FIGURE 1. Two fundamental niches defined by a pair of variables in a two-dimensional niche space. Only one species is supposed to be able to persist in the intersection subset region. The lines joining equivalent points in the niche space and biotop space indicate the relationship of the two spaces. The distribution of the two species involved is shown on the right hand panel with a temperature depth curve of the kind usual in a lake in summer.

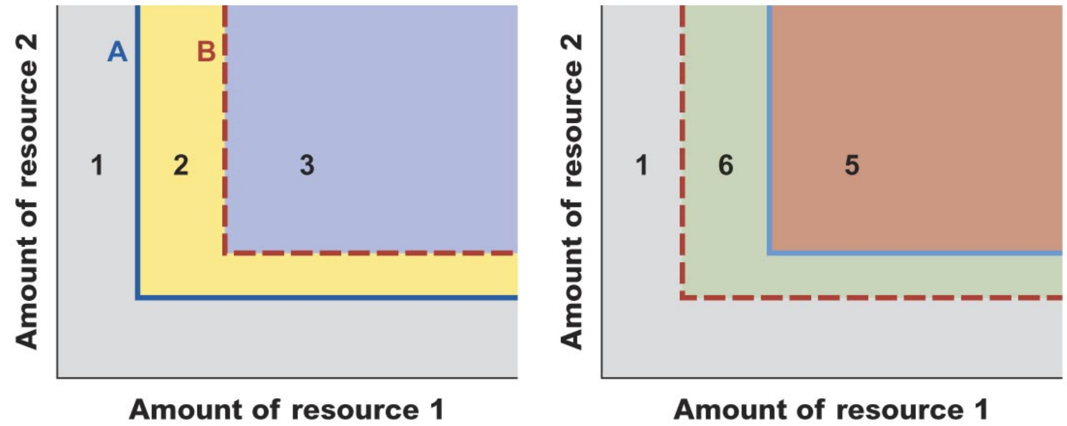


G. Evelyn Hutchinson

Fuente: Hutchinson, G. E. 1957. Cold Spring Harbor Symposia on Quantitative Biology 22: 415-427

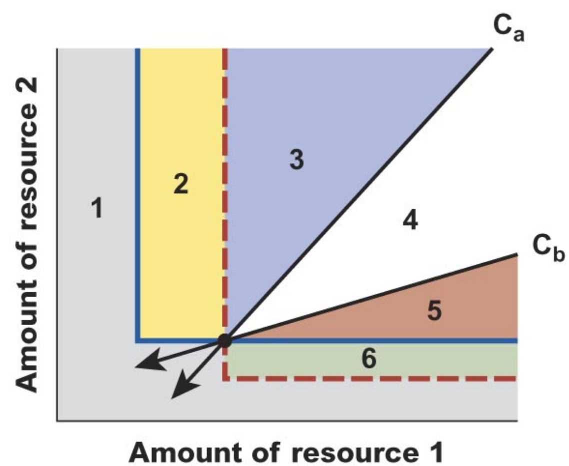
Modelo de competencia por recursos de Tilman



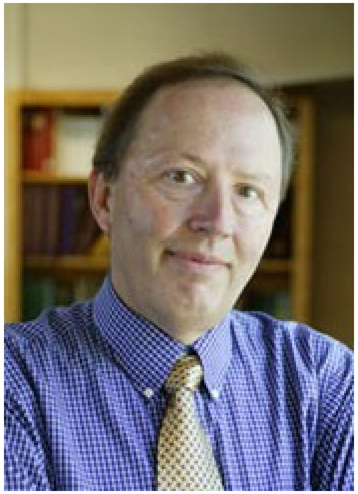


(a) Exclusion—species *A* wins.

(b) Exclusion—species *B* wins.



(c) Equilibrium coexistence.



David Tilman

Modelo de competencia por recursos de Tilman

En el Populus...

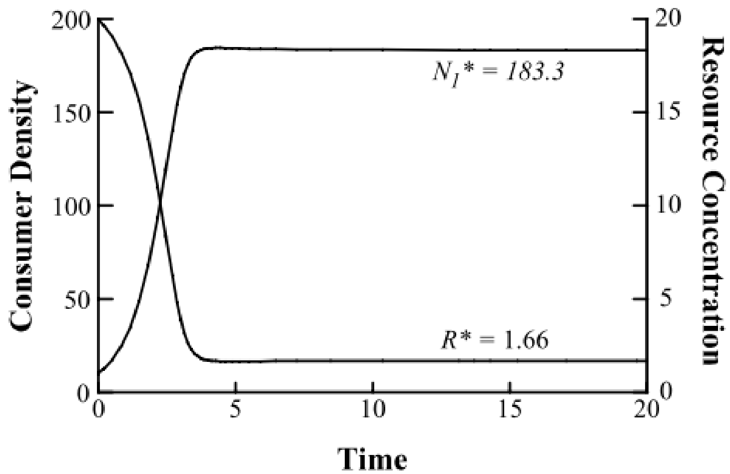
$$\frac{dR_j}{dt} = a_j\left(S_j - R_j\right) - \sum_i \left[N_i c_{ij} \left(\frac{dN_i}{N_i dt} + m_i \right) \right]$$ ← Recurso

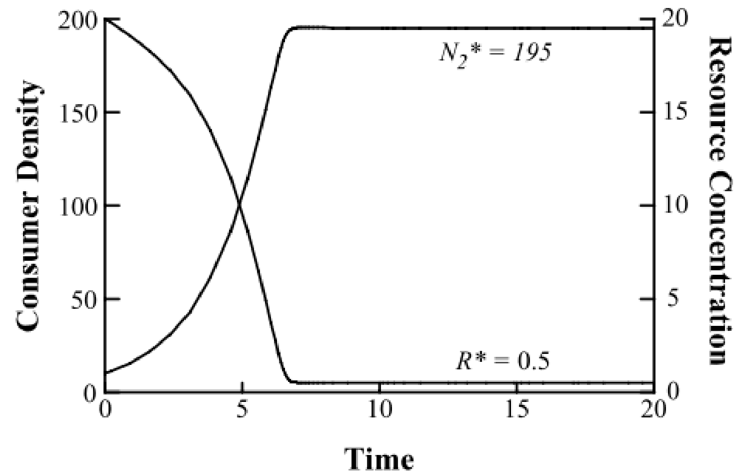
$$\frac{dN_i}{dt} = N_i \left[\frac{r_i R_j}{R_j + k_{ij}} - m_i \right]$$ ← Consumidor

Fuente: Populus Help

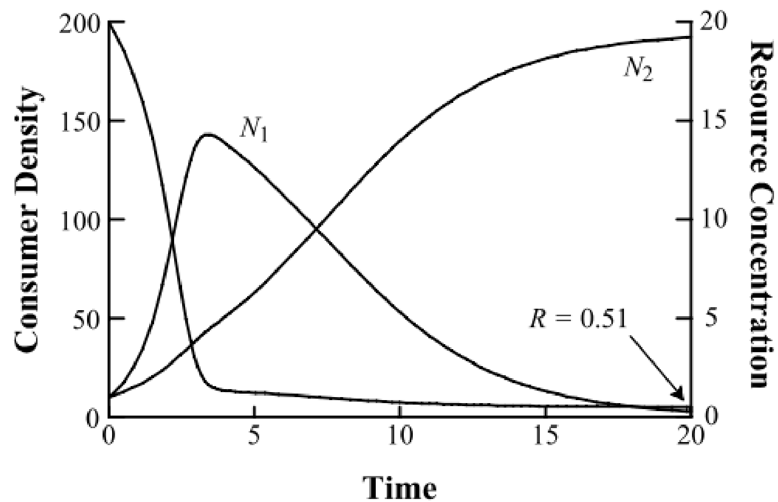
Modelo de competencia por recursos de Tilman

Competencia por un recurso:





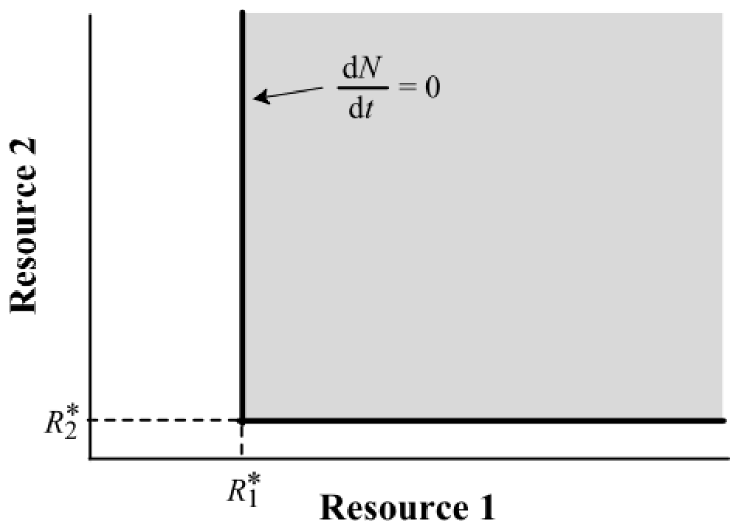
Gana la especie con *R** más bajo (la que puede persistir a una menor concentración del recurso).



Fuente: Populus Help

Modelo de competencia por recursos de Tilman

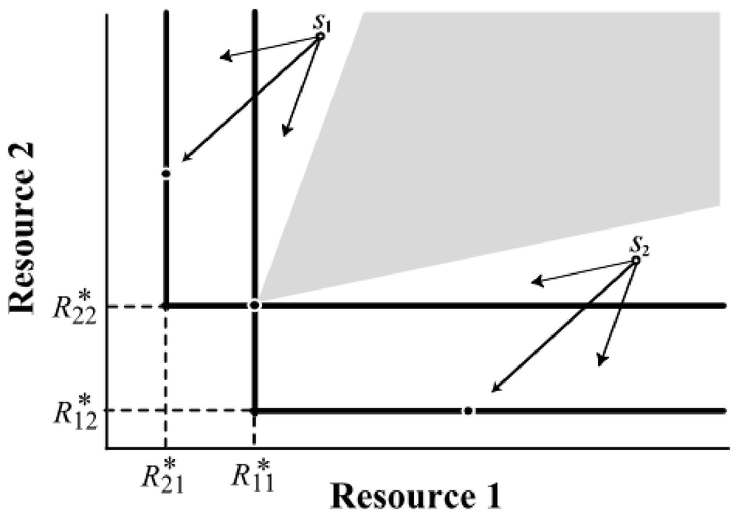
Competencia por dos recursos:



Fuente: Populus Help

Modelo de competencia por recursos de Tilman

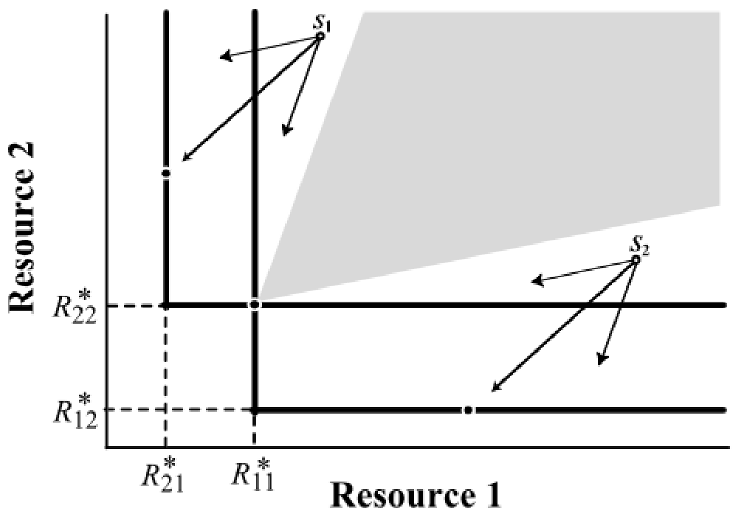
Competencia por dos recursos:



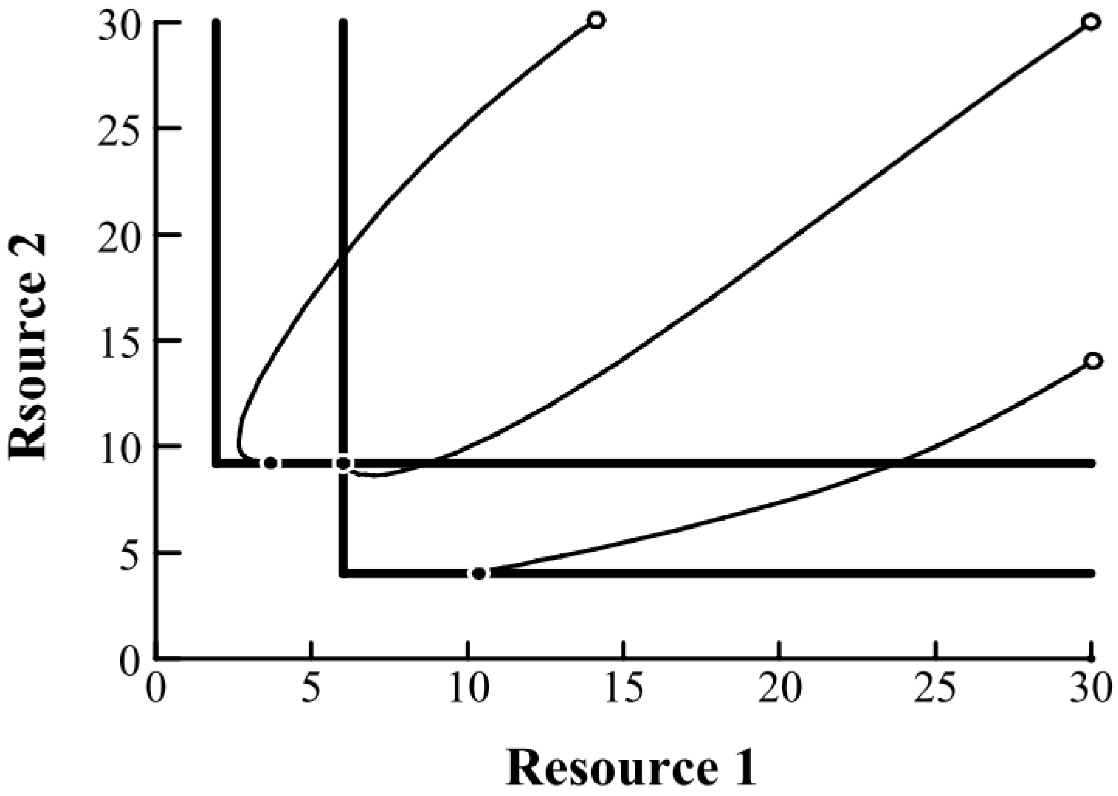
Fuente: Populus Help

Modelo de competencia por recursos de Tilman

Competencia por dos recursos:

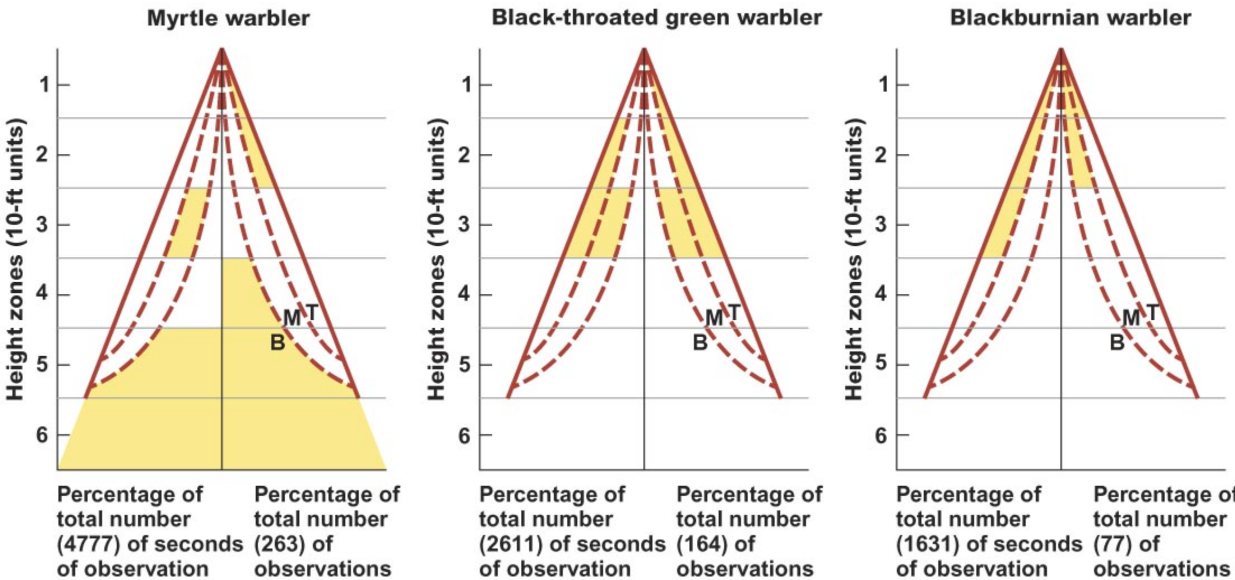
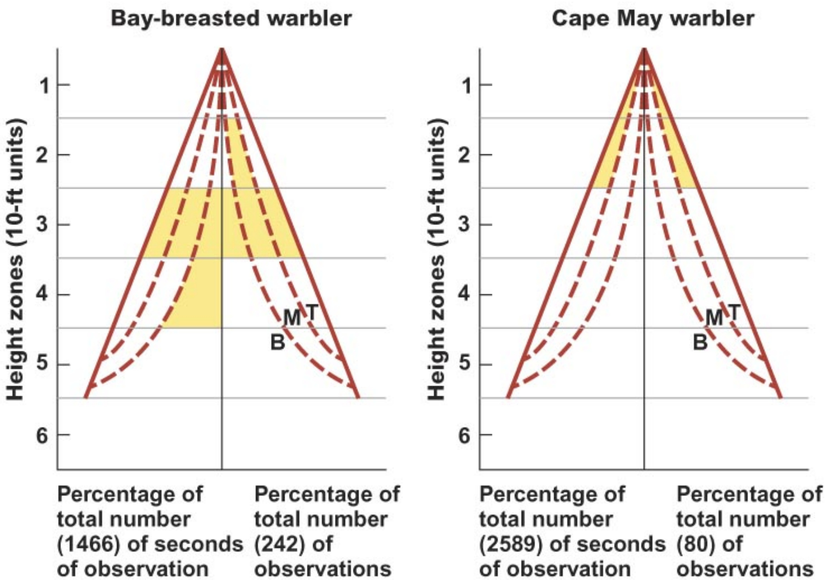


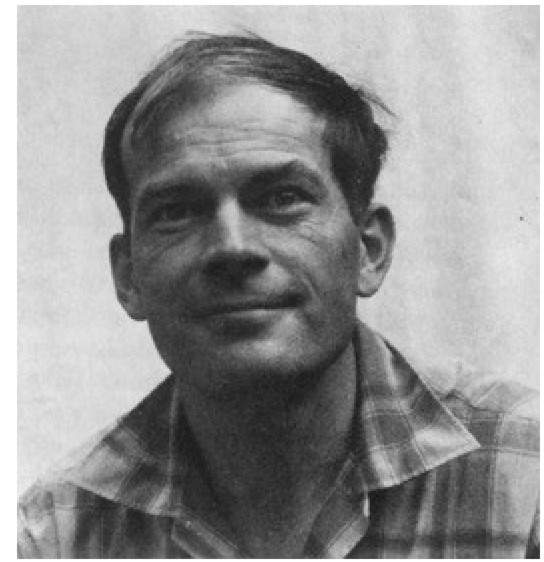
La coexistencia depende de la disponibilidad relativa de los dos recursos.



Fuente: Populus Help

Ejemplo: partición de nicho en “warblers”



Robert MacArthur

Ejemplo: competencia entre invertebrados intermareales

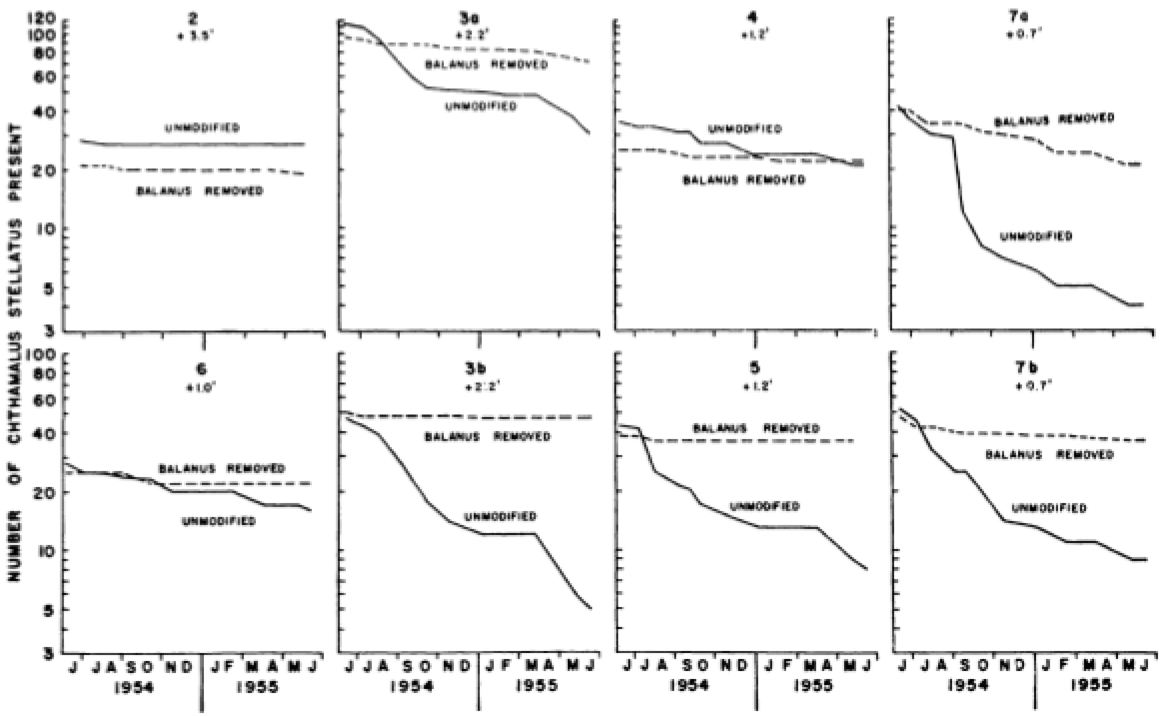


Fig. 2. Survivorship curves of *Chthamalus stellatus* which had settled naturally on the shore in the autumn of 1953. Areas designated "a" were protected from predation by cages. In each area the survival of *Chthamalus* growing without contact with *Balanus* is compared to that in the undisturbed area. For each area the vertical distance in feet from M.T.L. is shown.

Fuente: Connell (1961) Ecology 42: 710-723

Ejemplo: competencia entre invertebrados intermareales

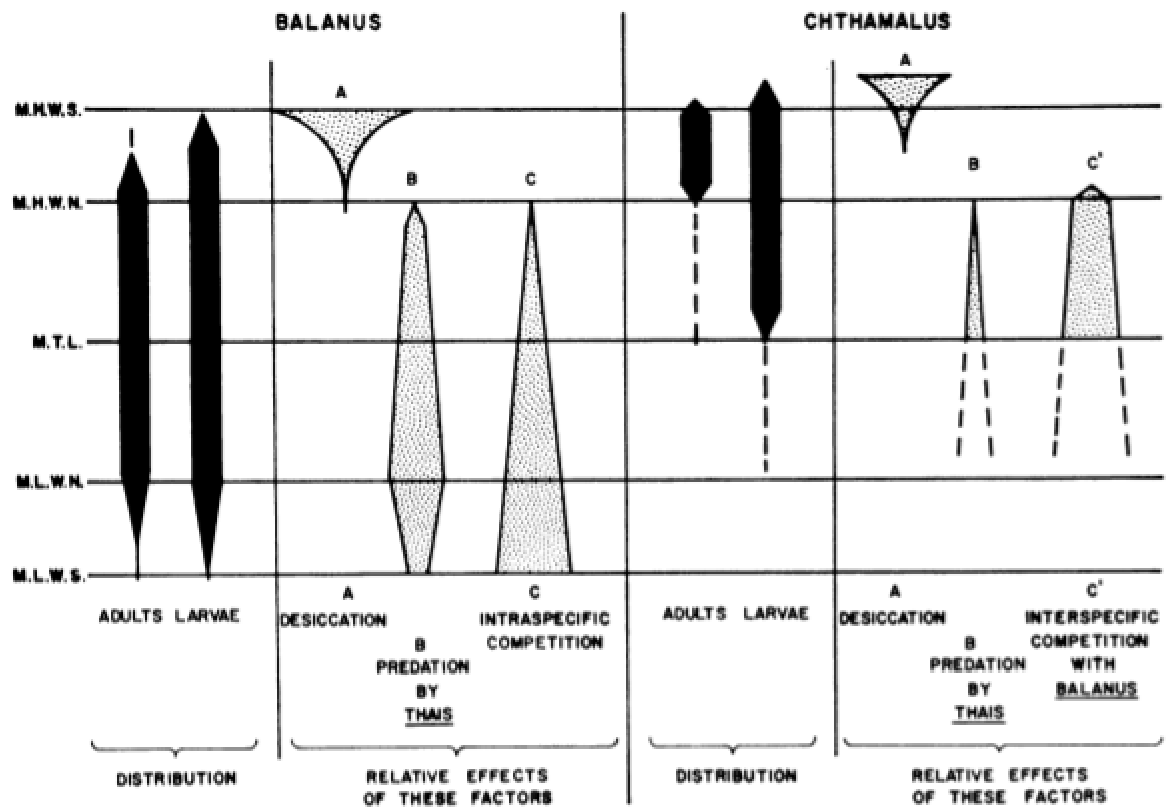


FIG. 5. The intertidal distribution of adults and newly settled larvae of *Balanus balanoides* and *Chthamalus stellatus* at Millport, with a diagrammatic representation of the relative effects of the principal limiting factors.

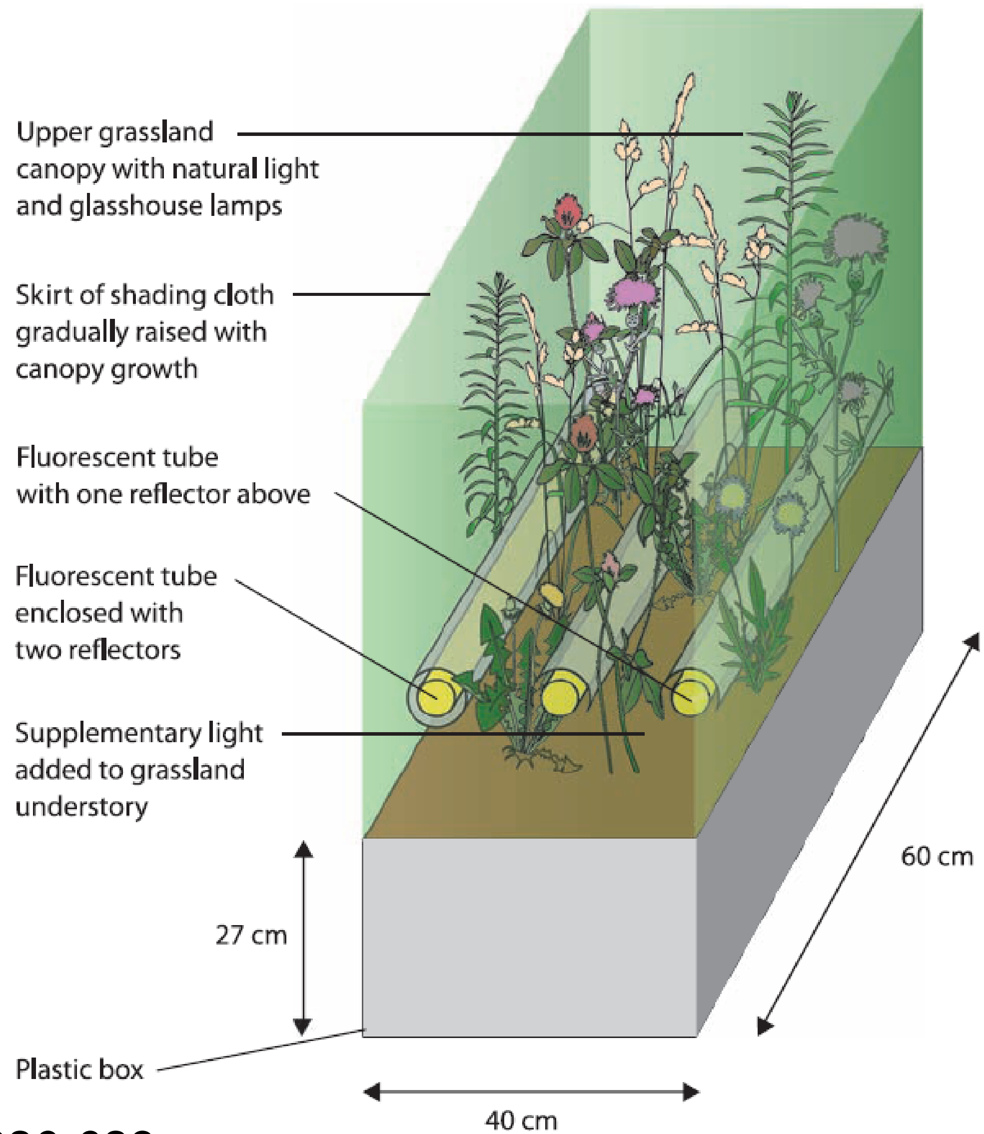
Fuente: Connell (1961) Ecology 42: 710-723

Eutorifización y competencia

Eutrofización en el mar Caspio. Fuente: Wikipedia.

Eutorifización y competencia

Fig. 1. Schematic representation of the experimental understory light addition. To save space, two open lights and one closed light are shown in the same experimental unit. The four treatment combinations were "control" (unfertilized, closed lights), "fertilization" (fertilized, closed lights), "light" (unfertilized, open lights), and "fertilization + light" (fertilized, open lights). For generality these four treatments were applied to four different plant communities, with each combination replicated twice ($n = 4 \times 4 \times 2 = 32$).



Fuente: Hautier et al. 2009. Science 324: 636-638

Eutorifización y competencia

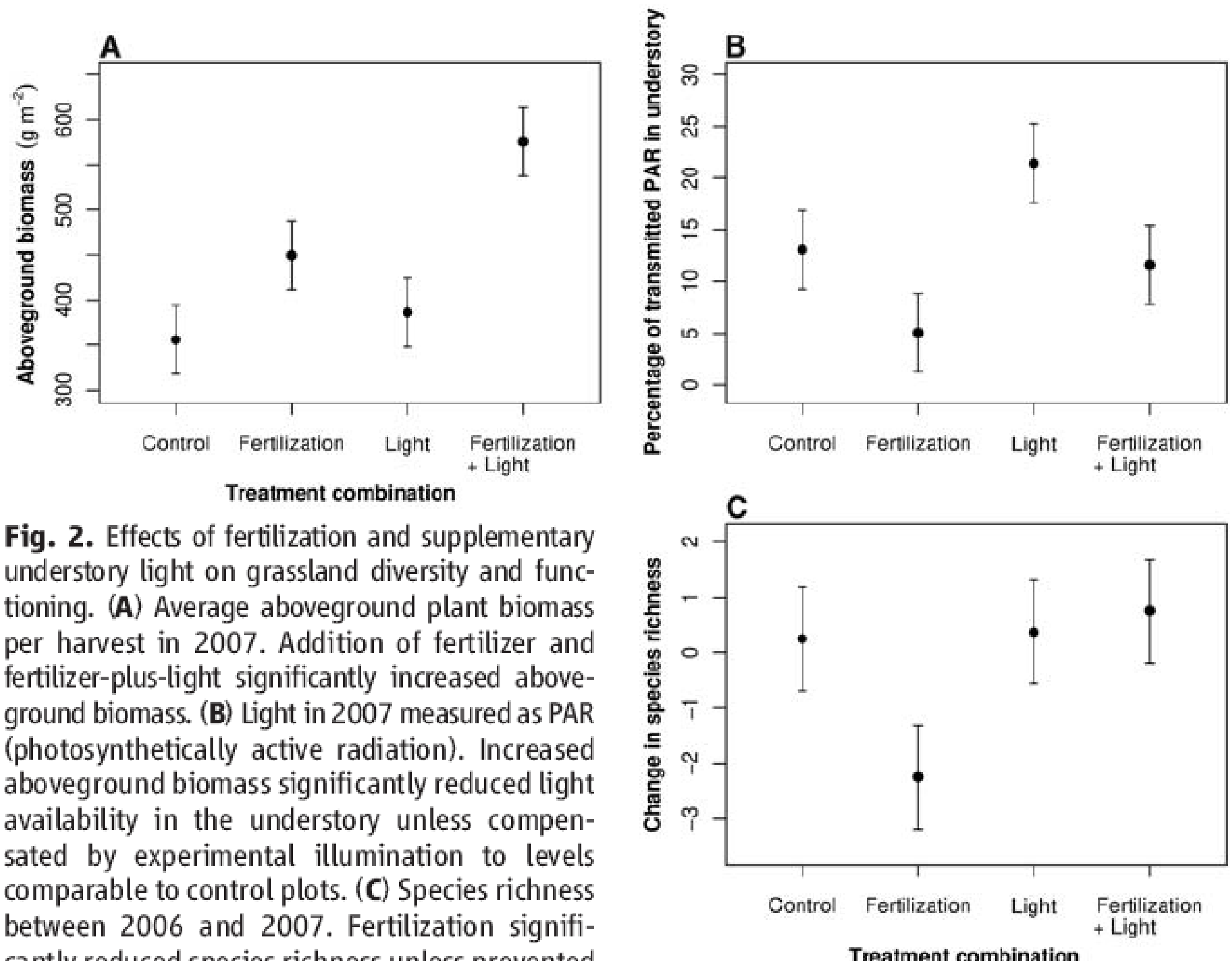
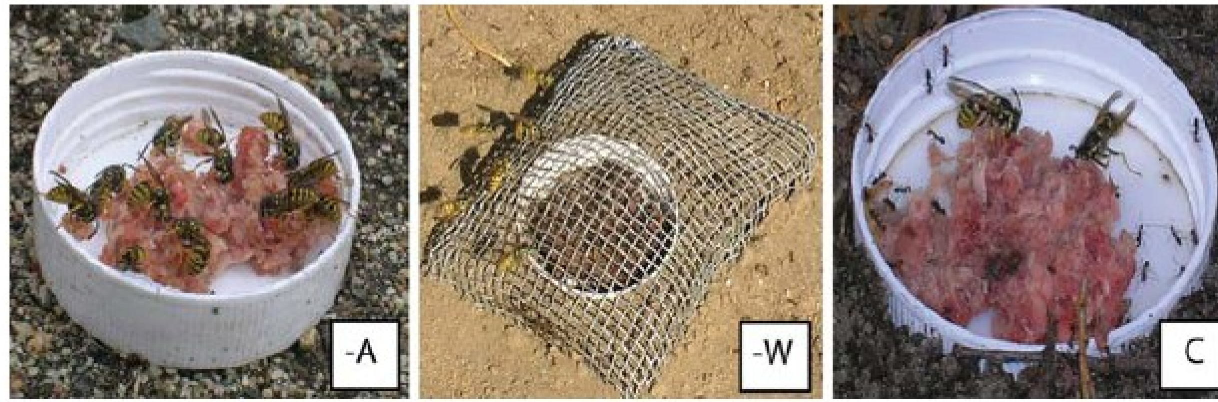


Fig. 2. Effects of fertilization and supplementary understory light on grassland diversity and functioning. (**A**) Average aboveground plant biomass per harvest in 2007. Addition of fertilizer and fertilizer-plus-light significantly increased aboveground biomass. (**B**) Light in 2007 measured as PAR (photosynthetically active radiation). Increased aboveground biomass significantly reduced light availability in the understory unless compensated by experimental illumination to levels comparable to control plots. (**C**) Species richness between 2006 and 2007. Fertilization significantly reduced species richness unless prevented by the addition of supplementary light to the understory. Points denote treatment means, and the intervals show least significant differences (treatments with nonoverlapping intervals are significantly different at $P = 0.05$).

Fuente: Hautier et al. 2009. Science 324: 636-638

Competencia entre nativas y exóticas

Fig. 1 Details on the sampling design. (−A) ant exclusion treatment, (−W) wasp exclusion treatment, and (C) control treatment. See text for further explanations. Photo credit: M. Masciocchi



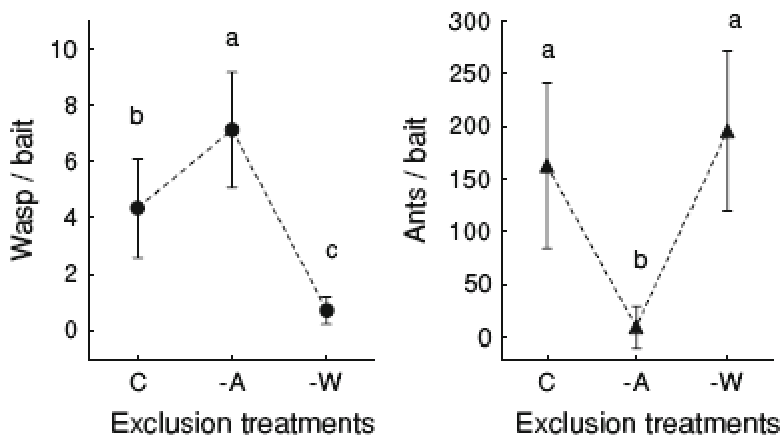


Fig. 2 Mean number (±1 SD) of wasps (left) and ants (right) per bait. Treatments are wasp exclusion (−W), ant exclusion (−A), and control (C). See further explanation in the text. Different lowercase letters imply statistically significant differences ($P < 0.01$, Fisher post hoc test). See Table 1 for ANOVA results

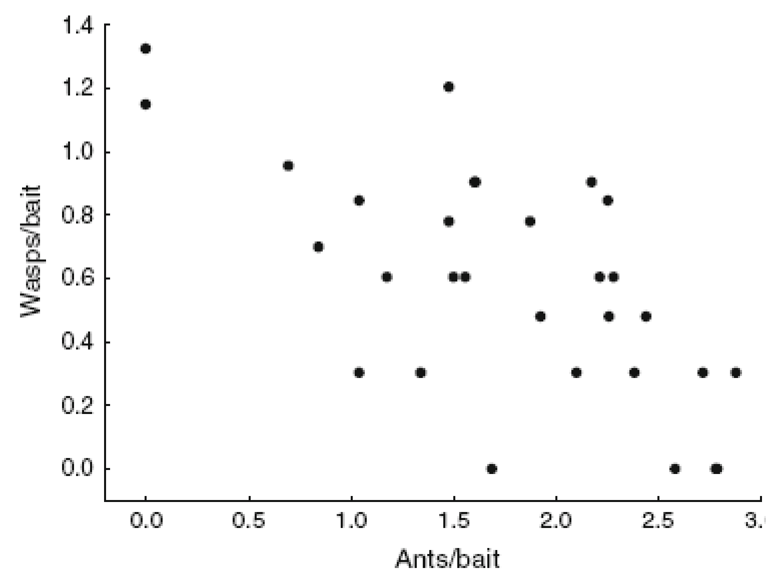
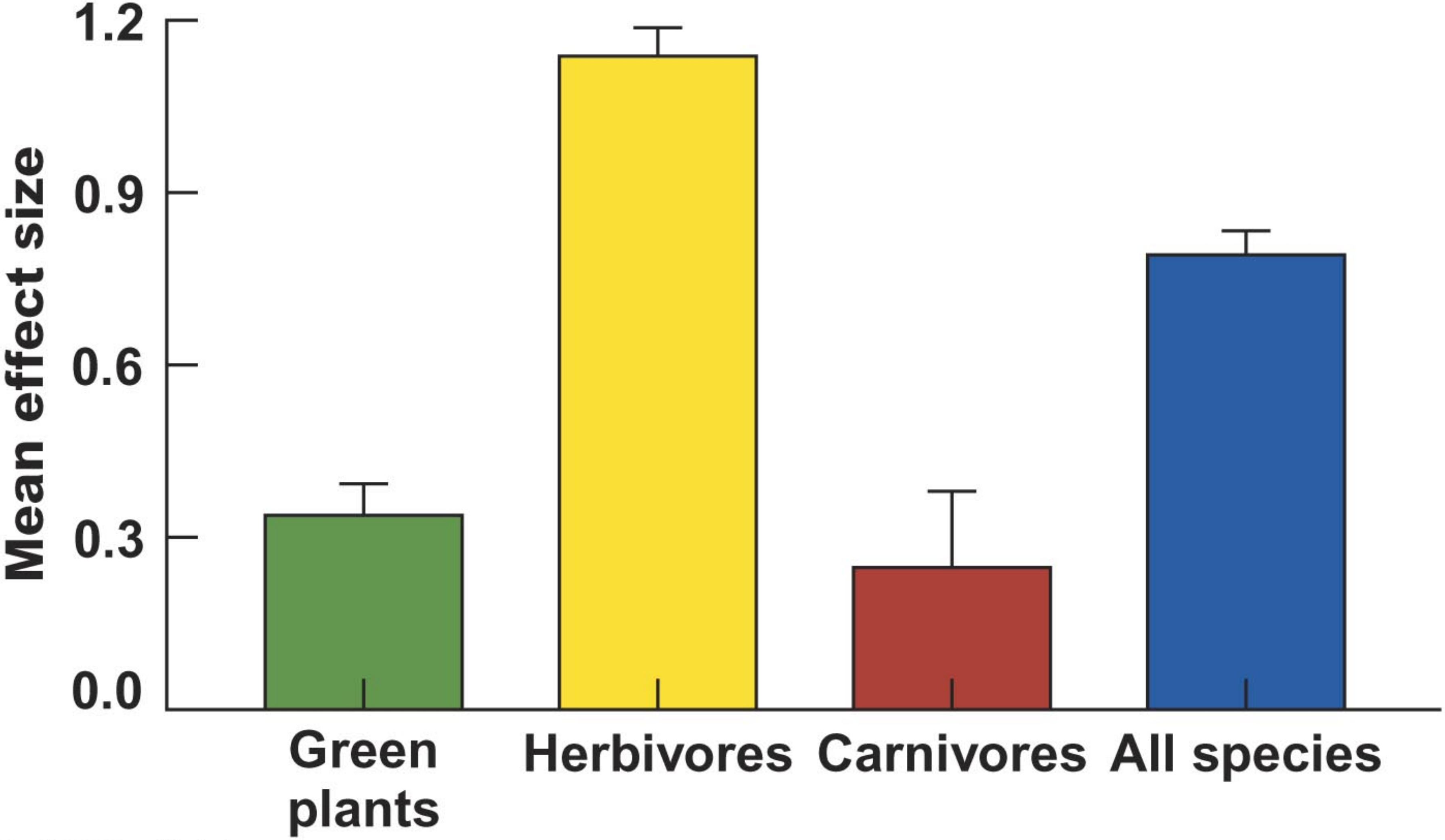


Fig. 3 Relationship between the number of wasps and ants per bait in control treatments. Each point represents a food bait. Data were transformed as $x' = \log(1 + x)$

Fuente: Masciocchi et al. 2010. Biological Invasions 12: 625-631

Evidencia para la competencia



Criterios para establecer si ocurre la competencia

Table 10.1 Criteria for establishing the occurrence of interspecific competition, listed according to the strength of the evidence for its occurrence in natural populations.

Criteria	Strength of evidence
1. Observed checkerboard patterns of distribution consistent with predictions	Weak
2. Species overlap in resource use	↓
3. Intraspecific competition occurs	Suggestive
4. Resource use by one species reduces availability to another species	↓
5. One or more species is negatively affected	Convincing
6. Alternative process hypotheses are not consistent with patterns	

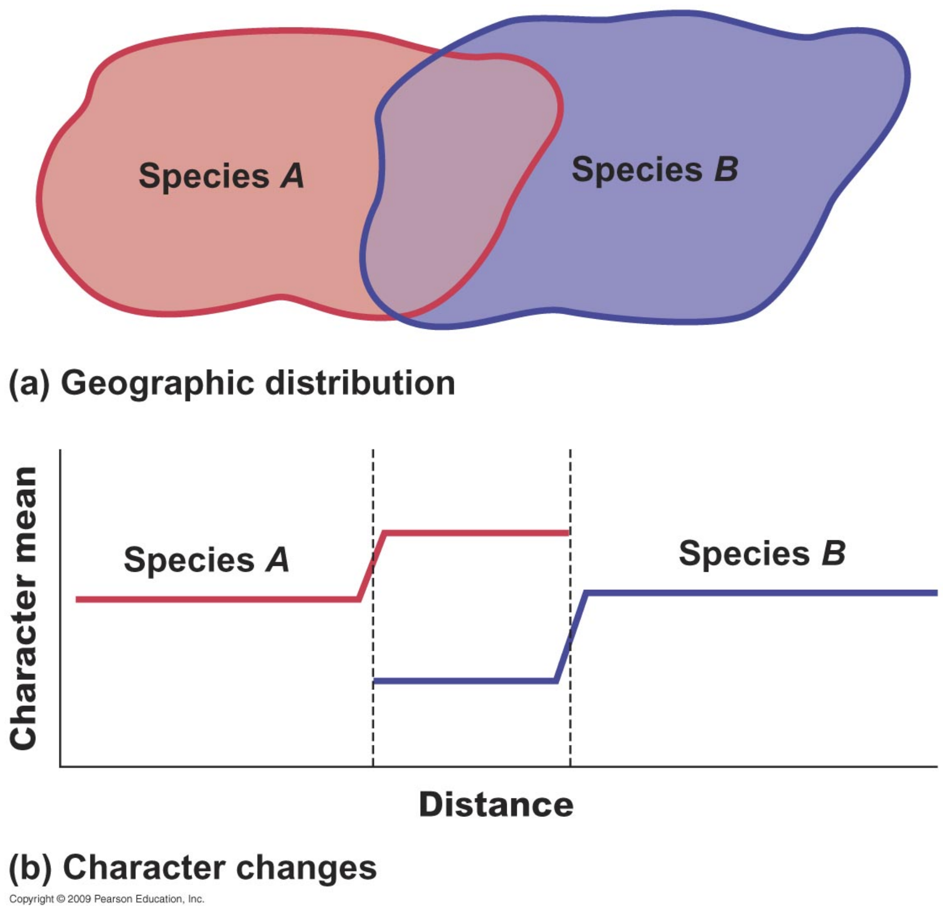
SOURCE: Wiens (1989), p. 17.

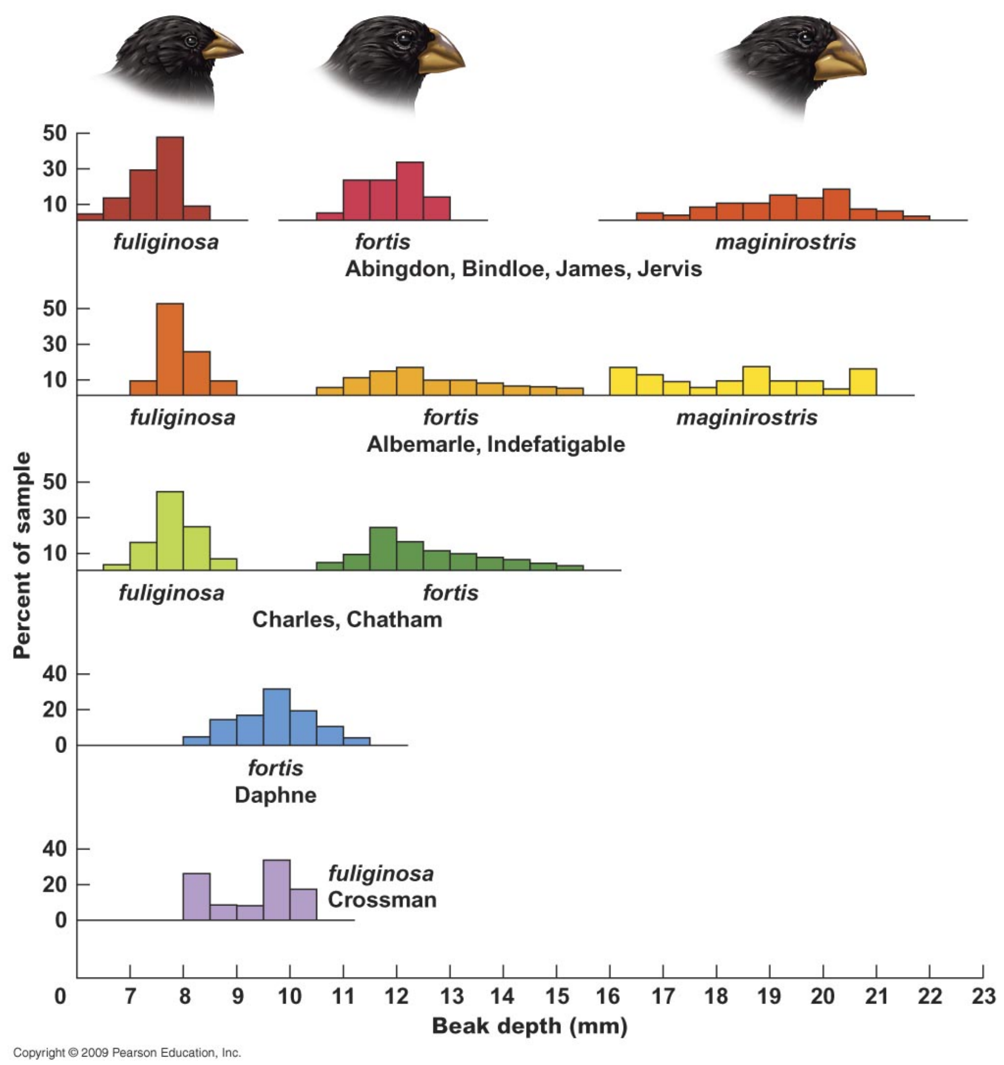
Competencia y evolución: selección *K* y *r*

Table 10.2 Characteristics of *r*-selected species and *K*-selected species. Many species will have characteristics intermediate between these two extreme life history strategies.

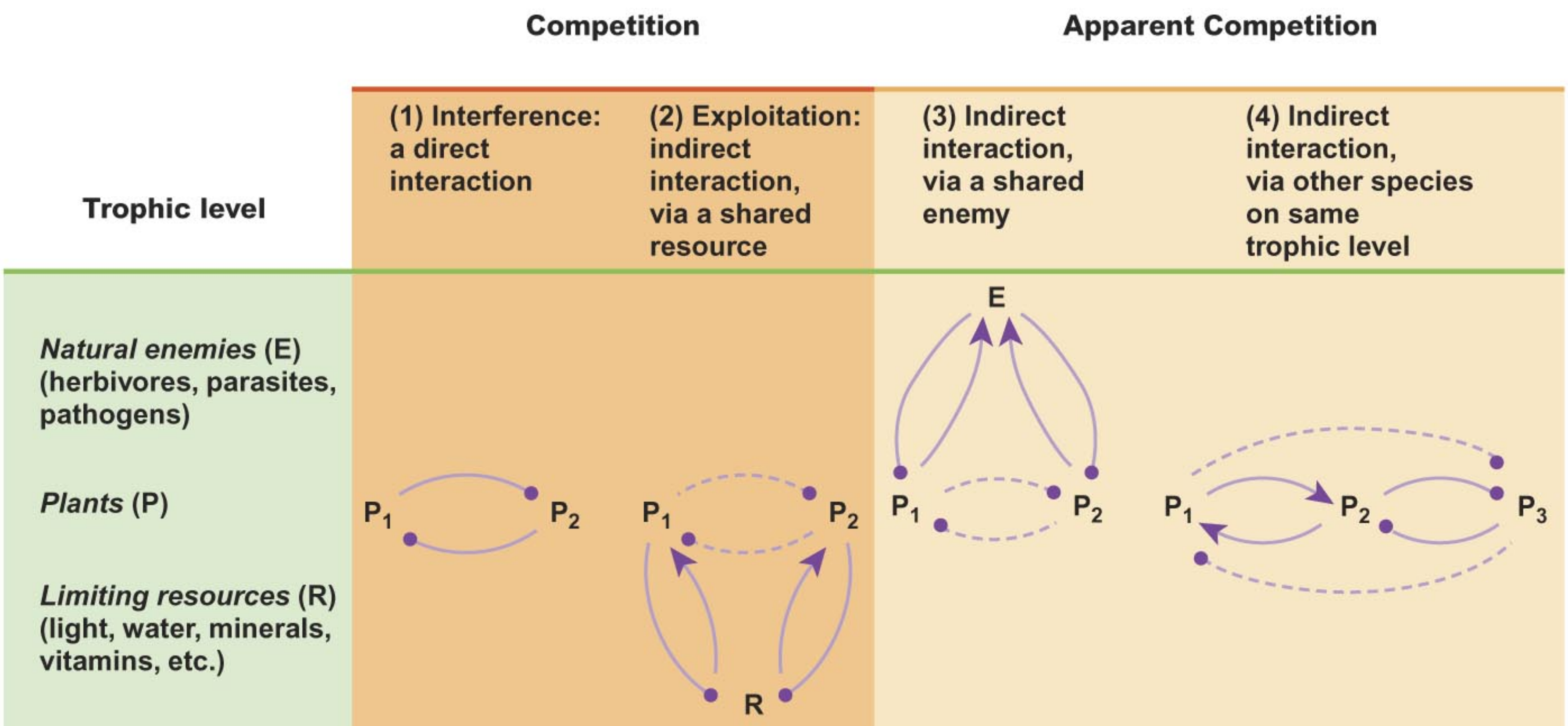
r-selected life history	*K*-selected life history
Small-sized organisms	Large-sized organisms
Many small reproductive units (seeds, spores, offspring)	Few larger reproductive units
Little energy used per reproductive unit	Much energy used to produce one reproductive unit
Early maturity	Late maturity and often parental care
Short expectation of life	Long life expectancy
Single reproductive episode (semelparous)	Many reproductive episodes (iteroparous)
Type 3 survival curve (Figure 8.6)	Type 1 or 2 survival curve

Desplazamiento de caracteres





Competencia difusa y efectos indirectos



Competencia difusa y efectos indirectos

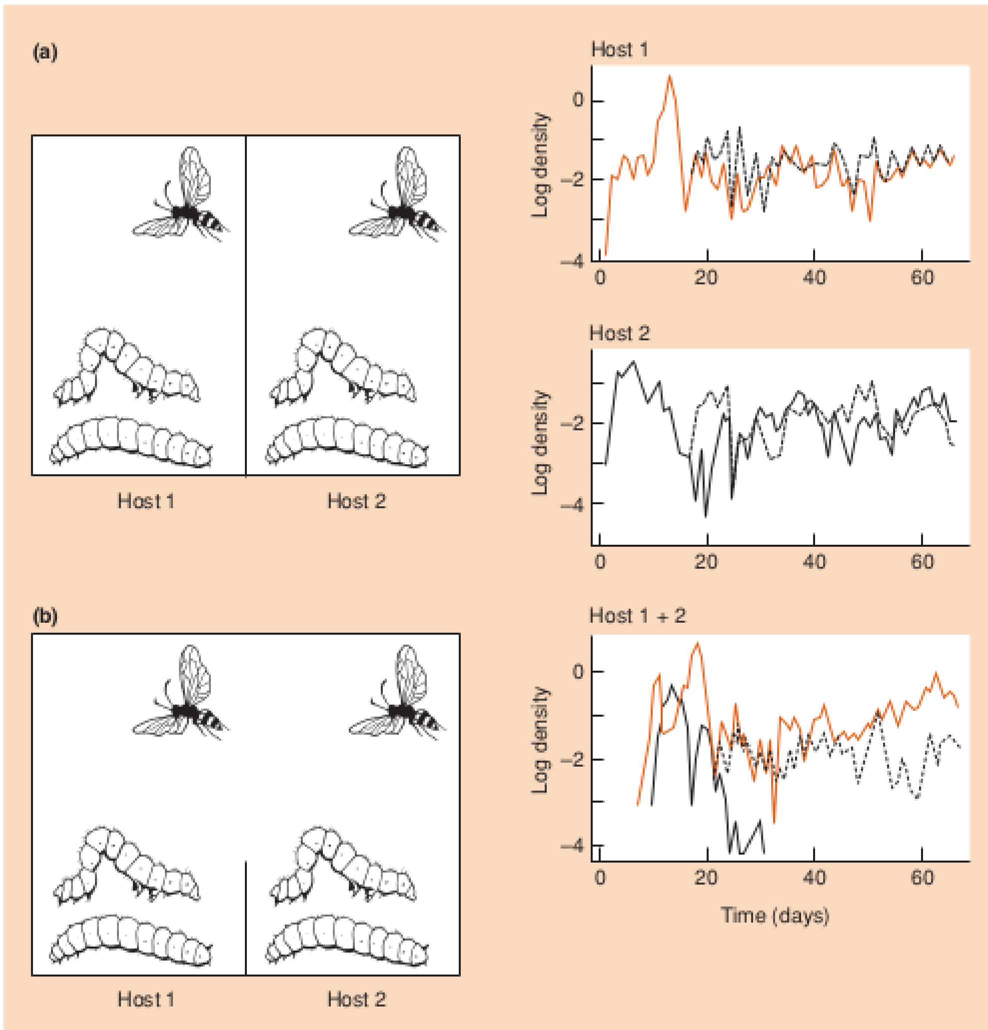


Figure 8.16 Parasite-mediated apparent competition via a parasitoid wasp *Venturia canescens* that lays eggs in two caterpillar host species. The experimental setups are illustrated on the left and the population dynamics of the parasitoid (dashed black lines) and host species (host 1 *Plodia interpunctella* (orange lines); host 2 *Ephestia kuehniella* (black lines)) on the right. (a) When only a single host was present, the parasitoid and host coexisted with stable dynamics. (b) When the parasitoid had access to both hosts, host 2 showed diverging oscillations and went extinct. (From Hudson & Greenman, 1998, after Bonsall & Hassell, 1997.)

Competencia difusa y efectos indirectos

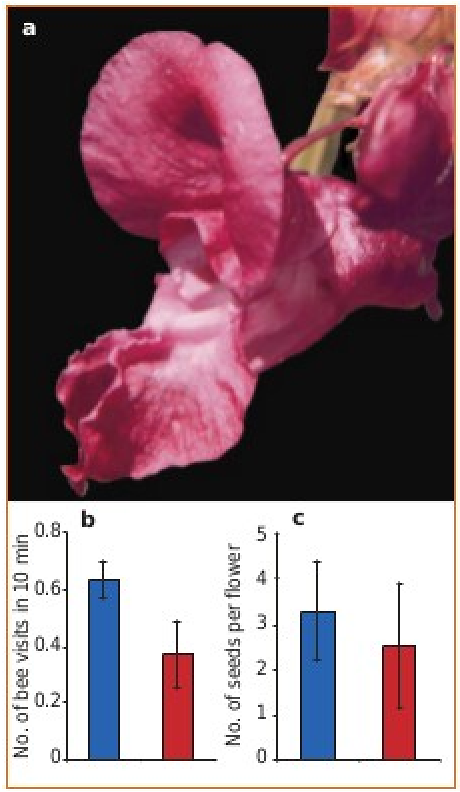


Figure 1 *Impatiens glandulifera*, an Asian beauty that has conquered Europe's river-banks. **a,** The strongly scented flowers of *I. glandulifera* are extremely rich in nectar and therefore very attractive to bumblebee pollinators. Photograph by J. Bitz. **b,** Pollinator visitation to *Stachys palustris* growing in uninterrupted patches (left) or in patches intermingled with *I. glandulifera* (right). **c,** Effect of the presence of *I. glandulifera* (right) on seed set of *S. palustris* (left, uninterrupted). *S. palustris* normally produces up to four seeds per flower. Error bars indicate standard deviation.

Fuente: Chittka & Schürkens (2001) Nature 411: 653

Teórica 5: Recapitulación

- La competencia entre especies puede resultar de la explotación de los mismos recursos o de la interferencia en el acceso a los recursos.
- Modelos matemáticos simples pueden ser útiles para analizar la competencia.
- La competencia es común en las poblaciones naturales.
- En tiempos evolutivos la competencia resulta en diferenciación de nicho (e.g., desplazamiento de caracteres).