

Teórica 10:

Interacciones en las comunidades

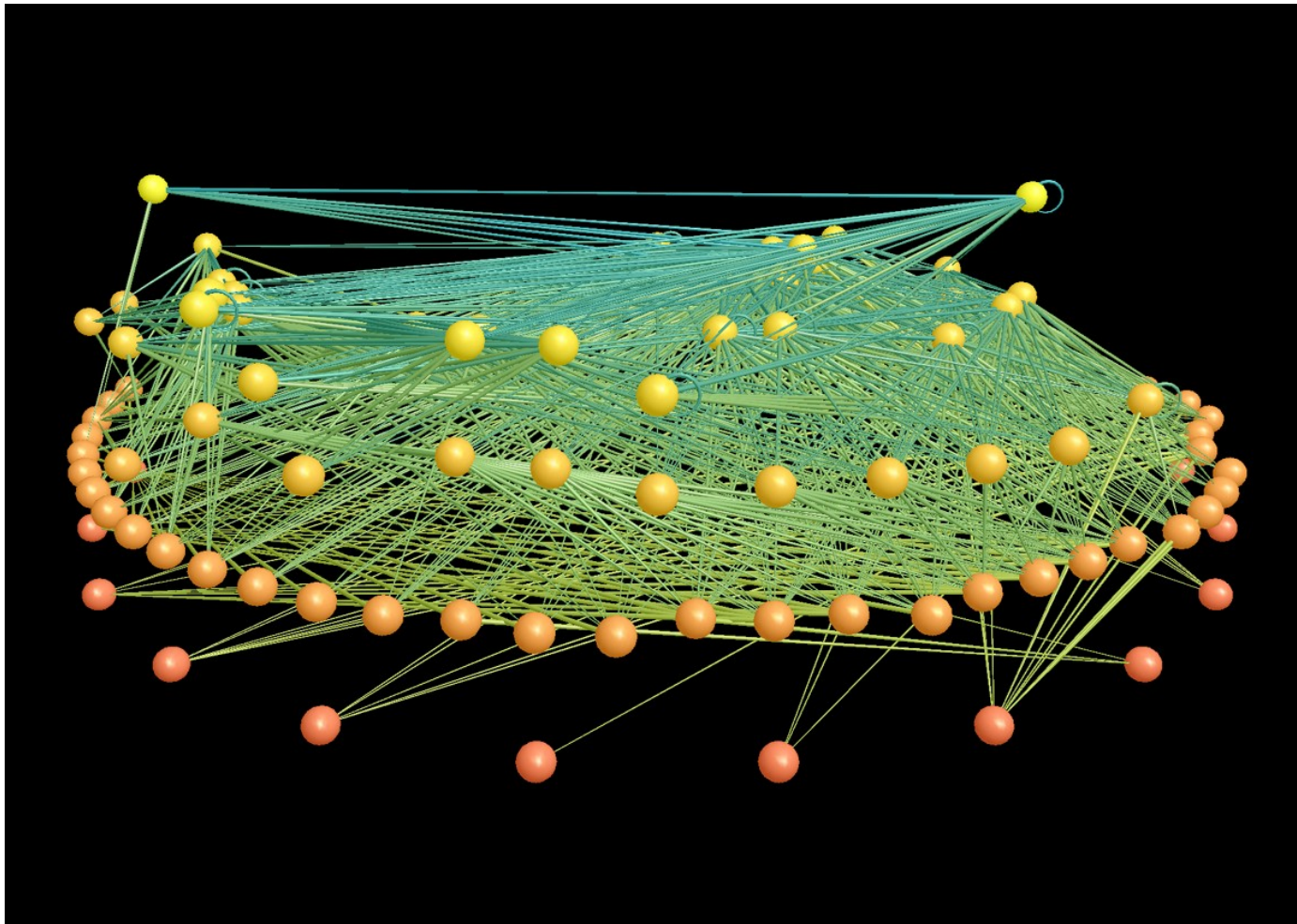
Repaso Teórica 9: Estructura comunitaria

- ¿Qué es una comunidad? ¿Atributos?
- ¿Cómo estimamos la diversidad de especies?
- ¿Qué procesos determinan la estructura comunitaria?
- ¿Cómo varía la biodiversidad geográficamente, y por qué?
- ¿Cómo varía la estructura comunitaria en el tiempo?

Teórica 10: Esquema conceptual

- Depredación como fuerza organizadora: redes tróficas
- Mutualismo como fuerza organizadora: redes mutualistas
- Modelos de organización comunitaria
- Importancia comunitaria: especies clave y especies dominantes
- Estabilidad comunitaria
- Biografía de islas

Redes tróficas



Red trófica de Little Rock Lake, Wisconsin, EE.UU. Fuente: Martínez N (1991) Ecol. Monogr. 61: 367–392.

Redes tróficas: definiciones

Table 20.1 Definitions of food web terminology.

Top predators: species eaten by nothing else in the food web (also called apex predators)

Basal species: species that feed on nothing within the web (usually plants)

Intermediate species: species that have both predators and prey within the web

Trophic species: groups of organisms that have identical sets of predators and prey

Cycles within a food web: species *A* eats species *B* and species *B* eats *A*

Cannibalism: a cycle in which a species feeds upon itself

Interactions: any feeding relationship (line with an arrow in a food web diagram)

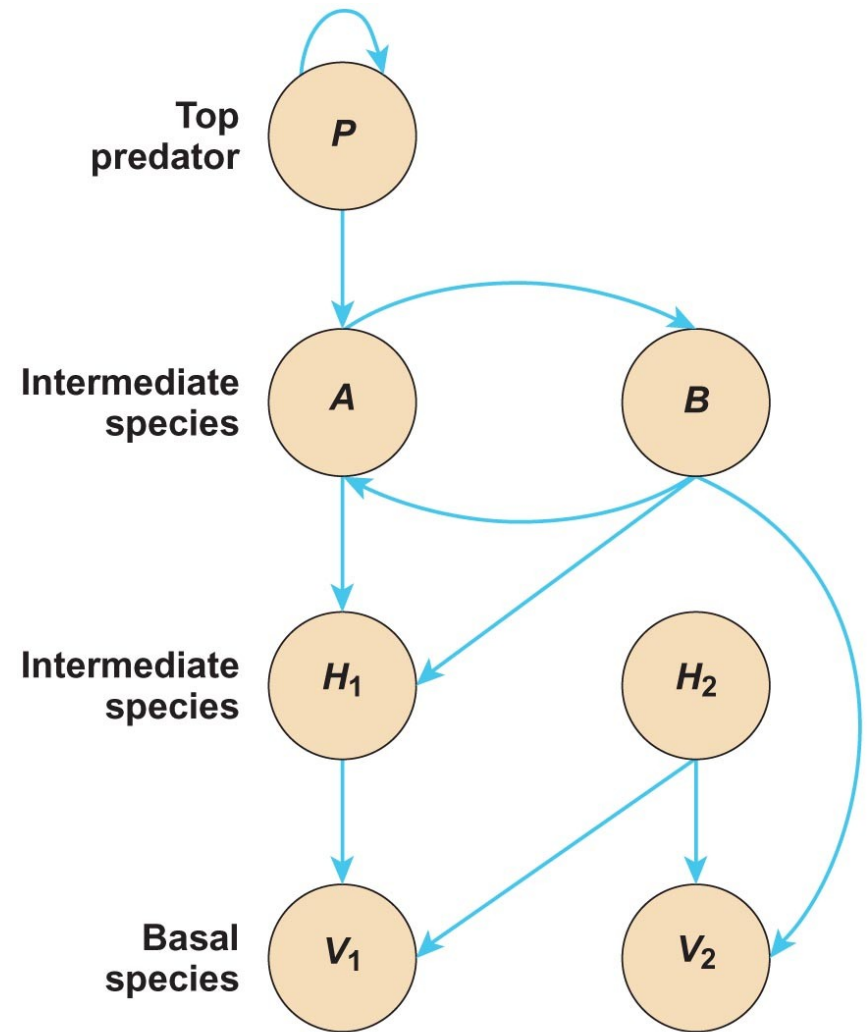
Possible interactions: among s species in a food web, there can be s^2 possible interactions, including cannibalism

Connectance: number of actual interactions in a food web divided by the number of possible interactions

Linkage density: average number of links or interactions per species in the web

Omnivores: species that feed on more than one trophic level

Compartments: groups of species with strong linkages among group members but weak linkages to other groups of species



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Figure 20.5 illustrates these definitions.

SOURCE: Modified from Cohen (1978) and Pimm (1982).

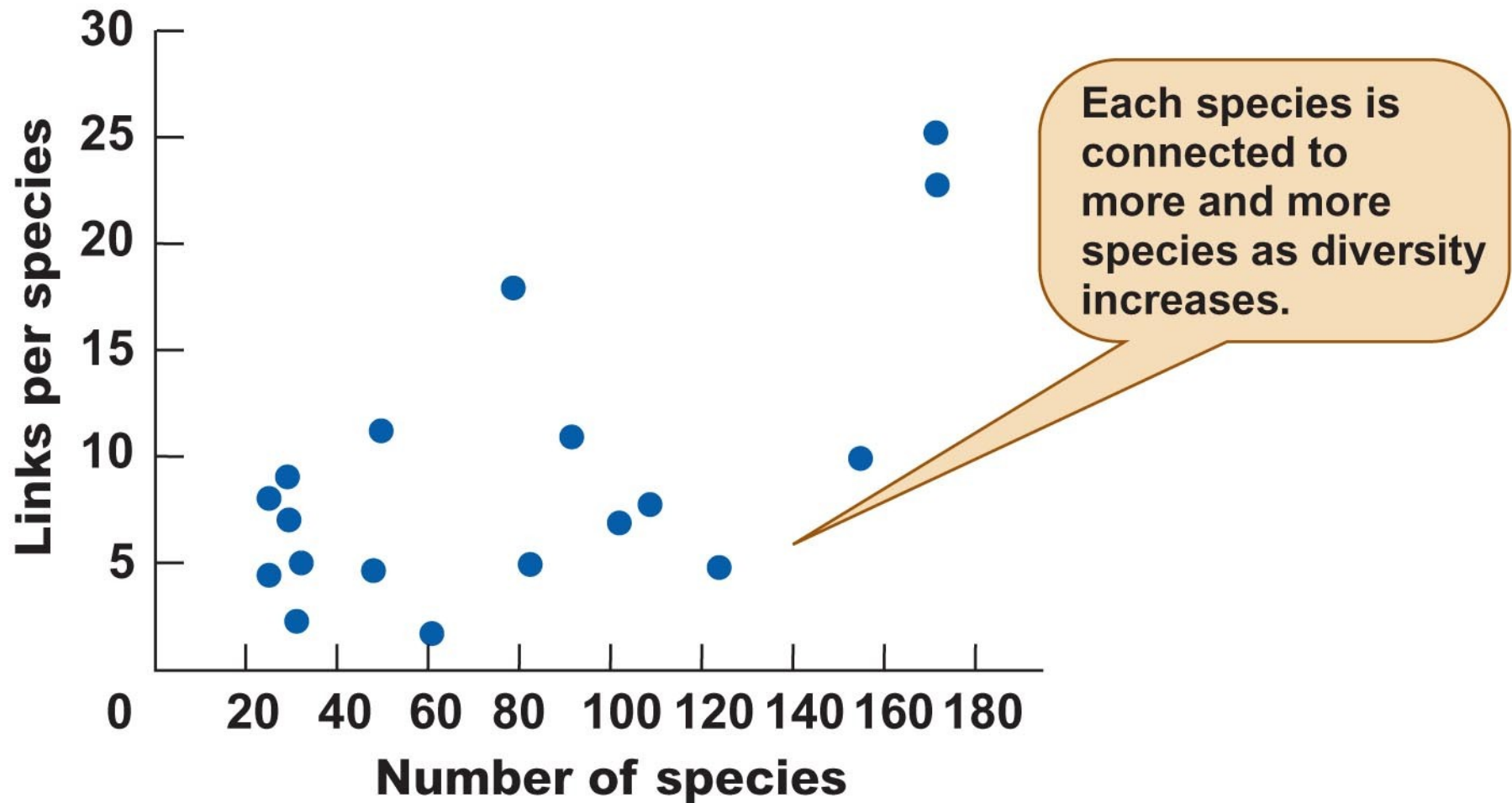
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Generalizaciones sobre redes tróficas

1. Relación positiva entre no. de enlaces y número de especies
2. Las cadenas tróficas son cortas (explicaciones: energía, equilibrio dinámico)
3. La proporción de depredadores tope, intermedios y especies basales es constante
4. La omnivoría es común
5. La mayoría de las interacciones son débiles, pocas fuertes

Generalización 1:

No. de enlaces vs. no. de especies



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Generalización 1:

No. de enlaces vs. no. de especies

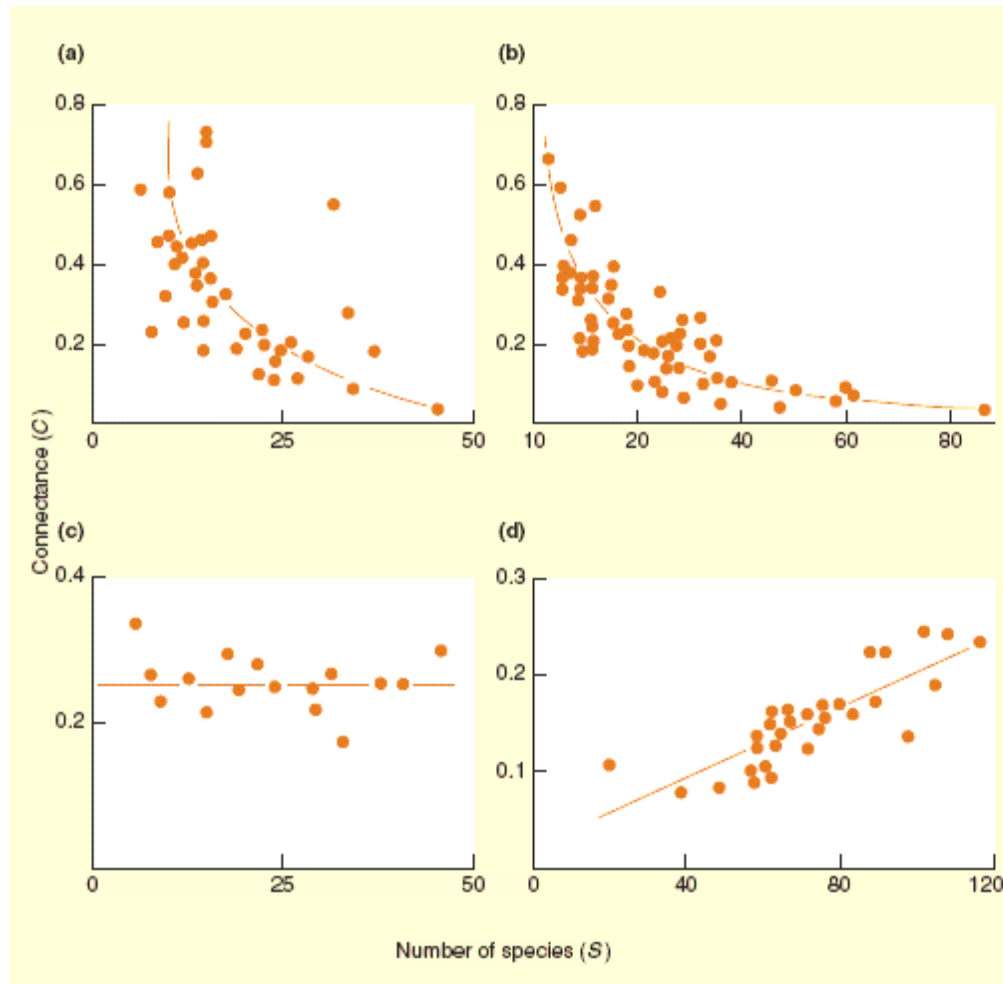
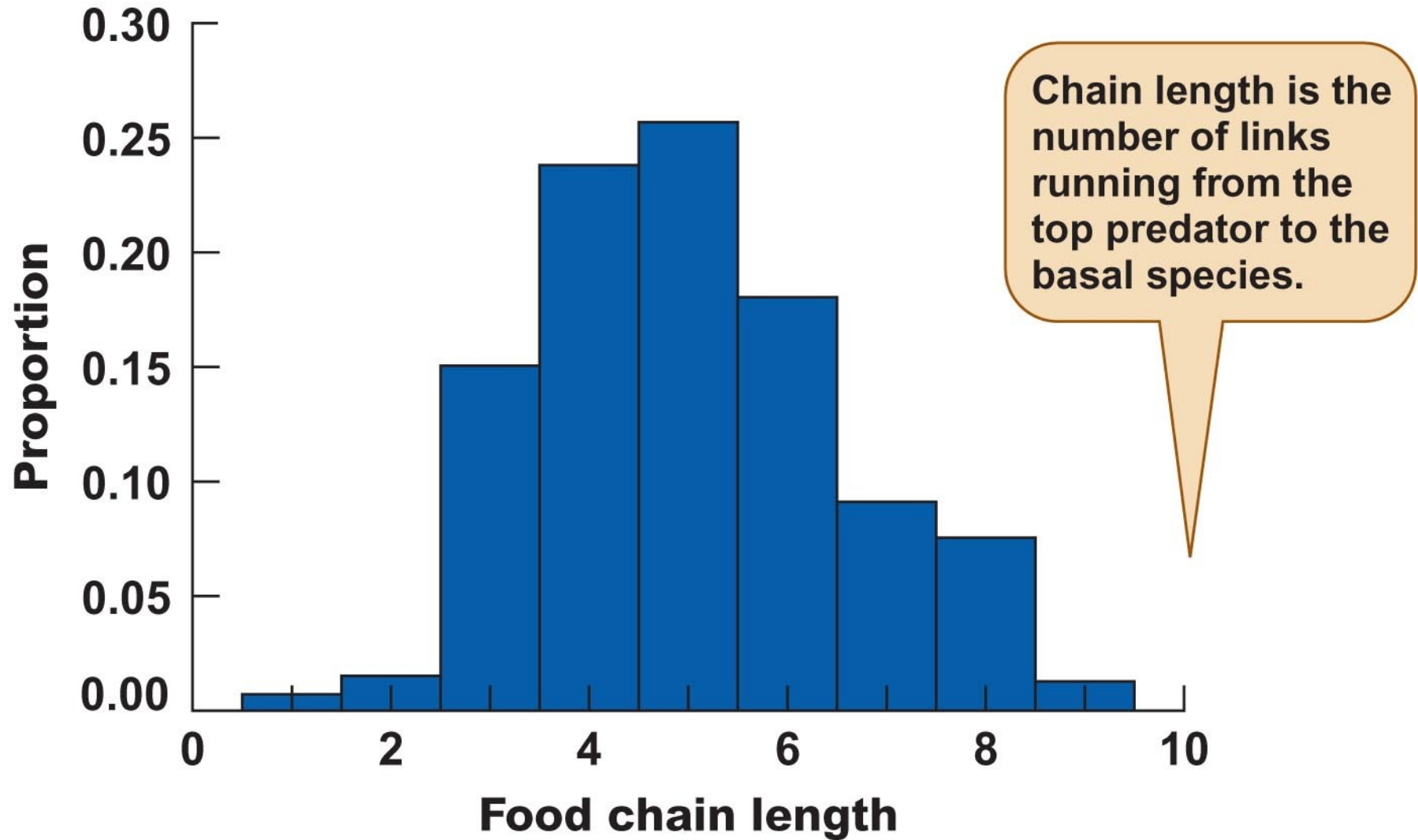


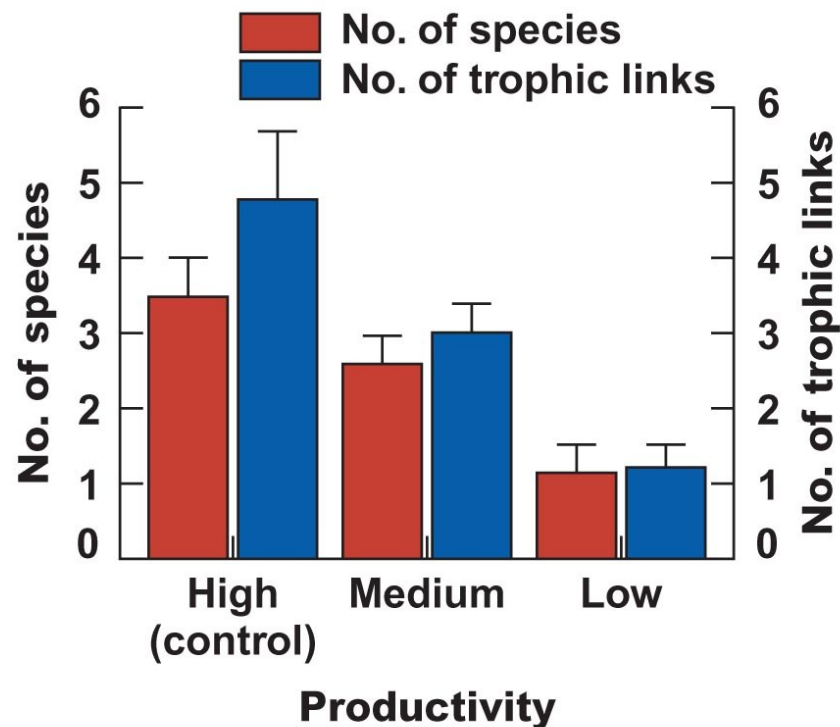
Figure 20.9 The relationships between connectance (C) and species richness (S). (a) For a compilation from the literature of 40 food webs from terrestrial, freshwater and marine environments. (After Briand, 1983.) (b) For a compilation of 95 insect-dominated webs from various habitats. (After Schoenly *et al.*, 1991.) (c) For seasonal versions of a food web for a large pond in northern England, varying in species richness from 12 to 32. (After Warren, 1989.) (d) For food webs from swamps and streams in Costa Rica and Venezuela. (After Winemiller, 1990.) ((a–d) after Hall & Raffaelli, 1993.)

Generalización 2:

Largo de las cadenas



Explicaciones del largo de las cadenas: energía vs. dinámica poblacional



Productivity in these tree-hole communities can be manipulated easily by adding leaf litter.



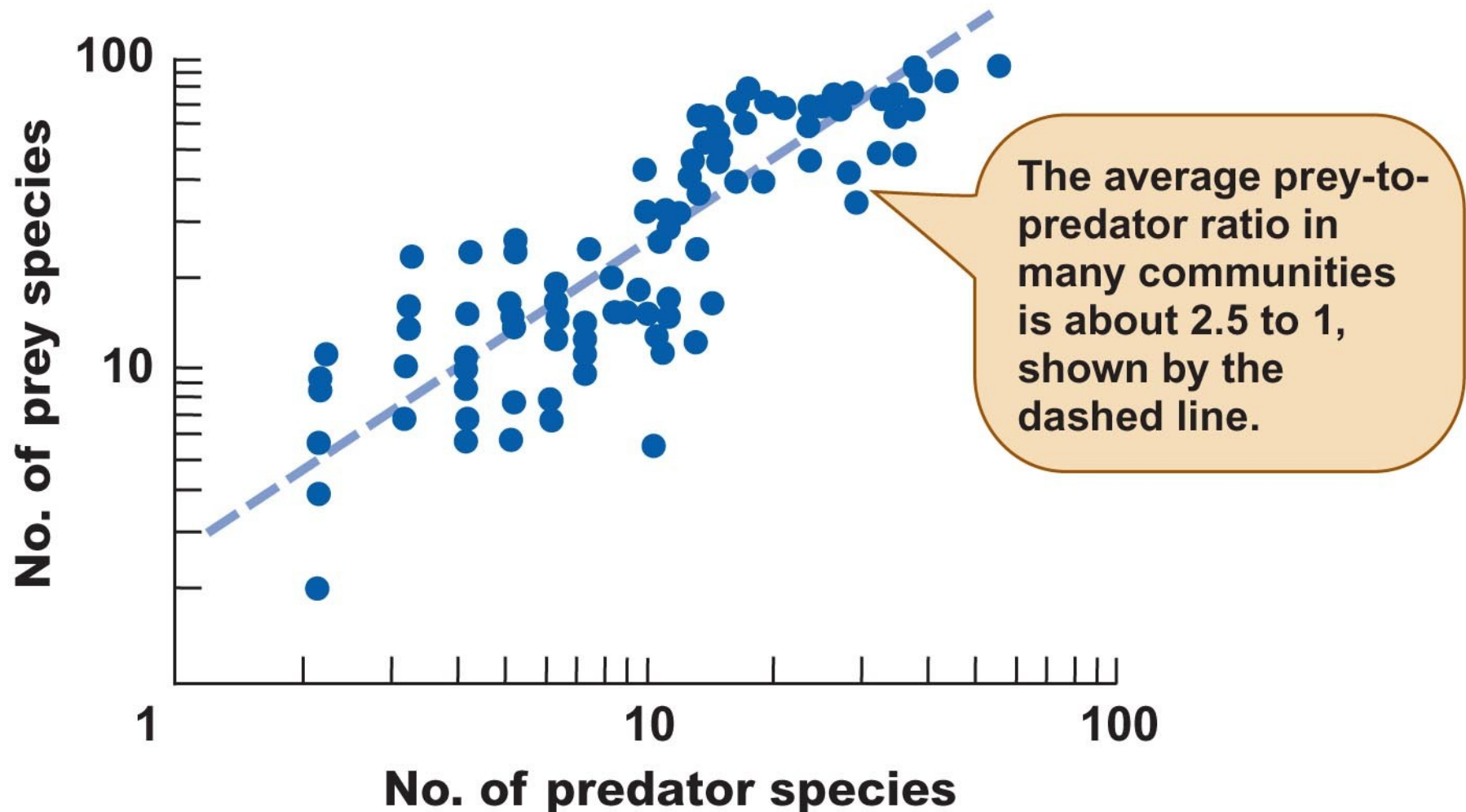
Chironomid larva



Mosquito larva

Generalización 3:

Proporción constante de especies tope, intermedias y basales



Generalización 4:

La omnivoría es común

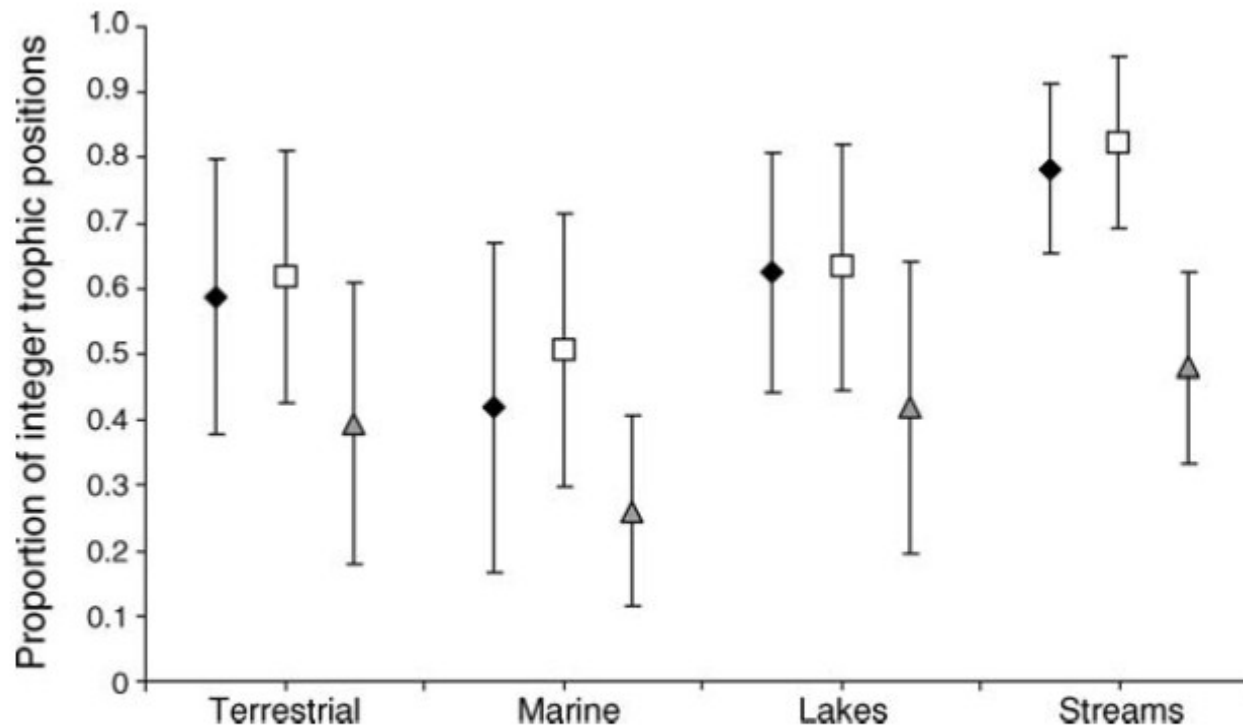


FIG. 2. Mean proportions ($\pm$ SD) of non-basal taxa with trophic positions that were integers for the four ecosystems. Data are shown for real food webs (black diamonds), randomized food webs that randomize secondary and higher consumers (white squares), and all non-plant taxa randomized (gray triangles).

Generalización 5: Muchas interacciones débiles, pocas fuertes

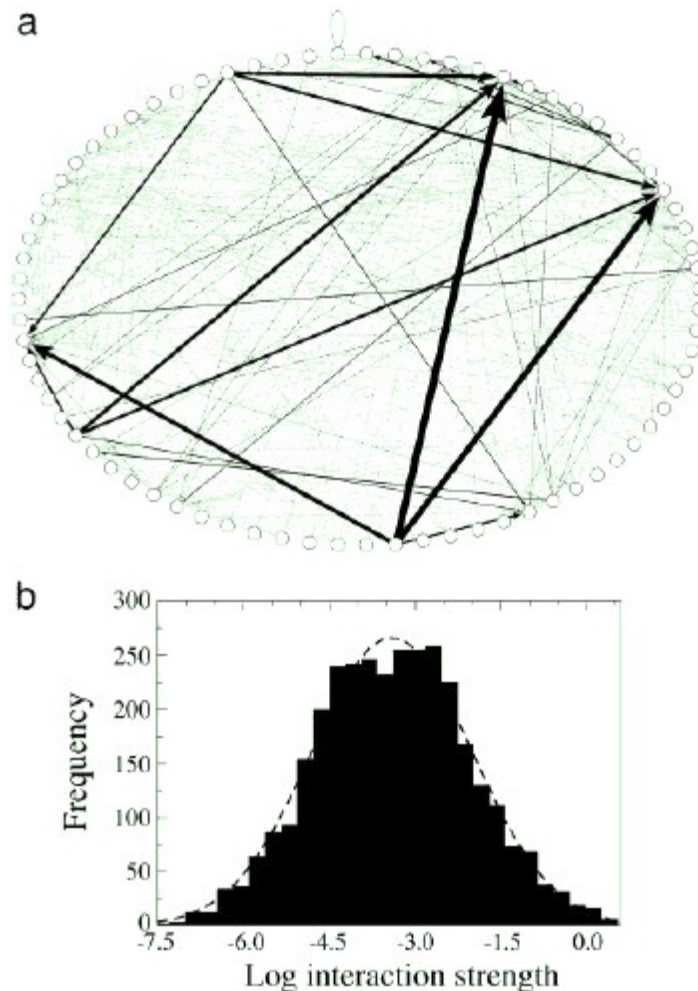


Fig. 2. Interaction strength variability. (a) Random sample of the Caribbean food web containing 30% of the species and 11% of the interactions. Each node represents a species or taxon. Arrows represent trophic interactions between predators and their prey. Arrow thickness is proportional to the interaction strength. Loops represent cannibalism. (b) Frequency distribution of interaction strengths ($n = 3,313$) spanning seven orders of magnitude. The line represents the best fit to a lognormal distribution.

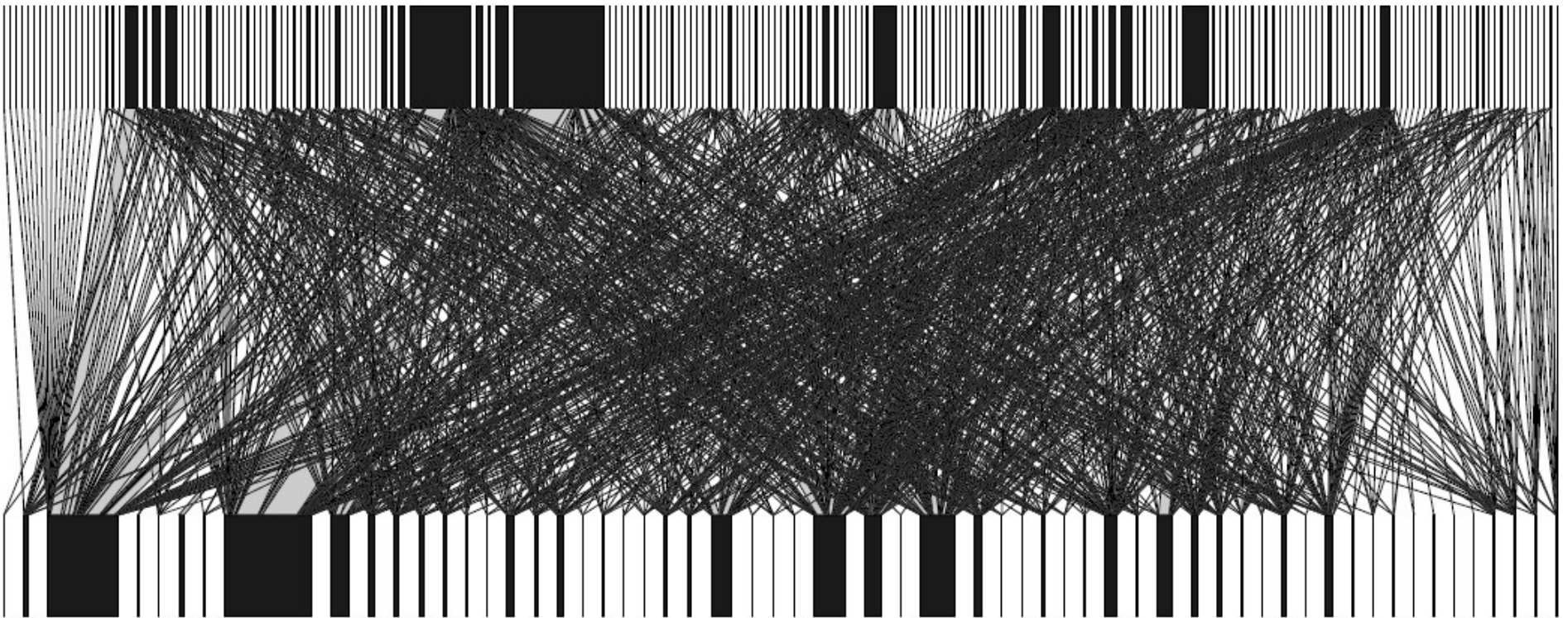
Fuente: Bascompte et al. ¹³
(2005) PNAS 102: 5443-5447

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Redes mutualistas

Polinizadores



Plantas

Red planta-polinizador de Villavicencio, Mendoza, Argentina. Fuente: Chacoff, Resasco, Vázquez (2018), Ecology 99: 21-28.

Generalización 1. Pocas interacciones potenciales ocurren realmente (baja conectancia)

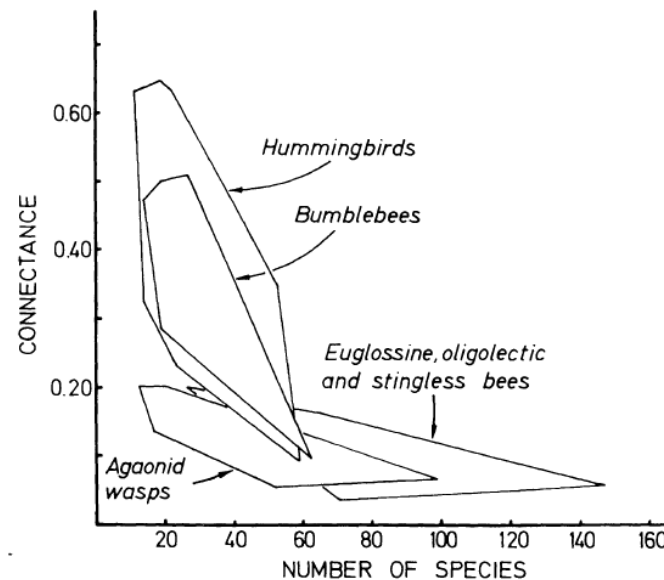


FIG. 2.—Connectance decreases with increasing species richness in plant-pollinator mutualisms. Differences in connectance values for different types of pollinators suggest specific modes of interaction (polygons include the range of values for different groups; see table 1).

Jordano (1987) Am. Nat. 129: 657-677

Generalización 2. Pocas especies con muchas interacciones, muchas con pocas

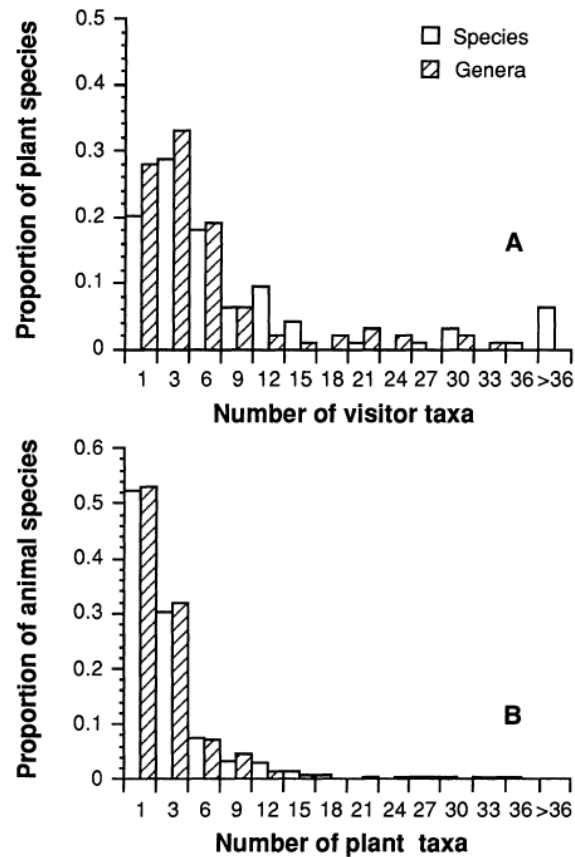


FIG. 2. Plant and pollinator records from Pikes Peak, Colorado (USA), from records in Clements and Long (1923). (A) Frequency distribution of the proportions of 94 native plant species receiving visits from different numbers of animal species and genera. (B) Frequency distribution of the proportions of 268 native animal species visiting different numbers of plant species and genera.

con pocas

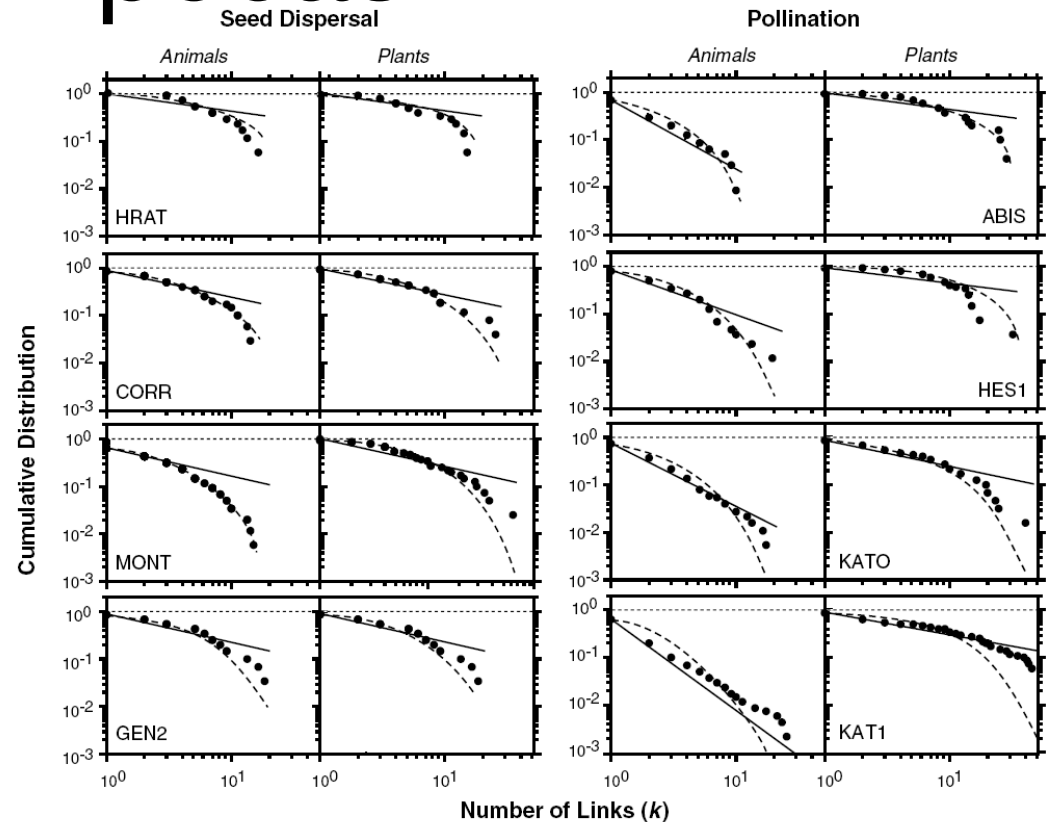
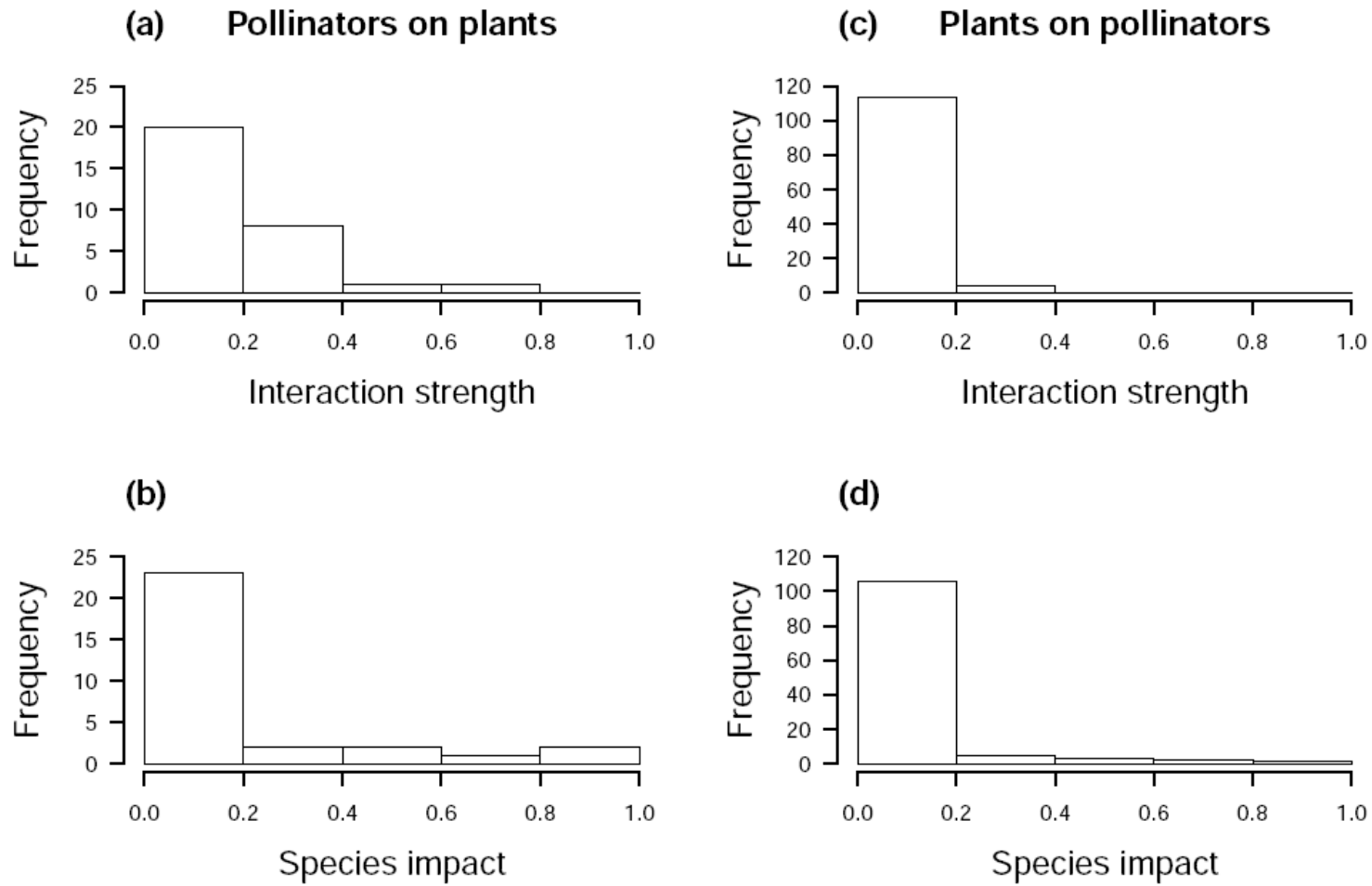
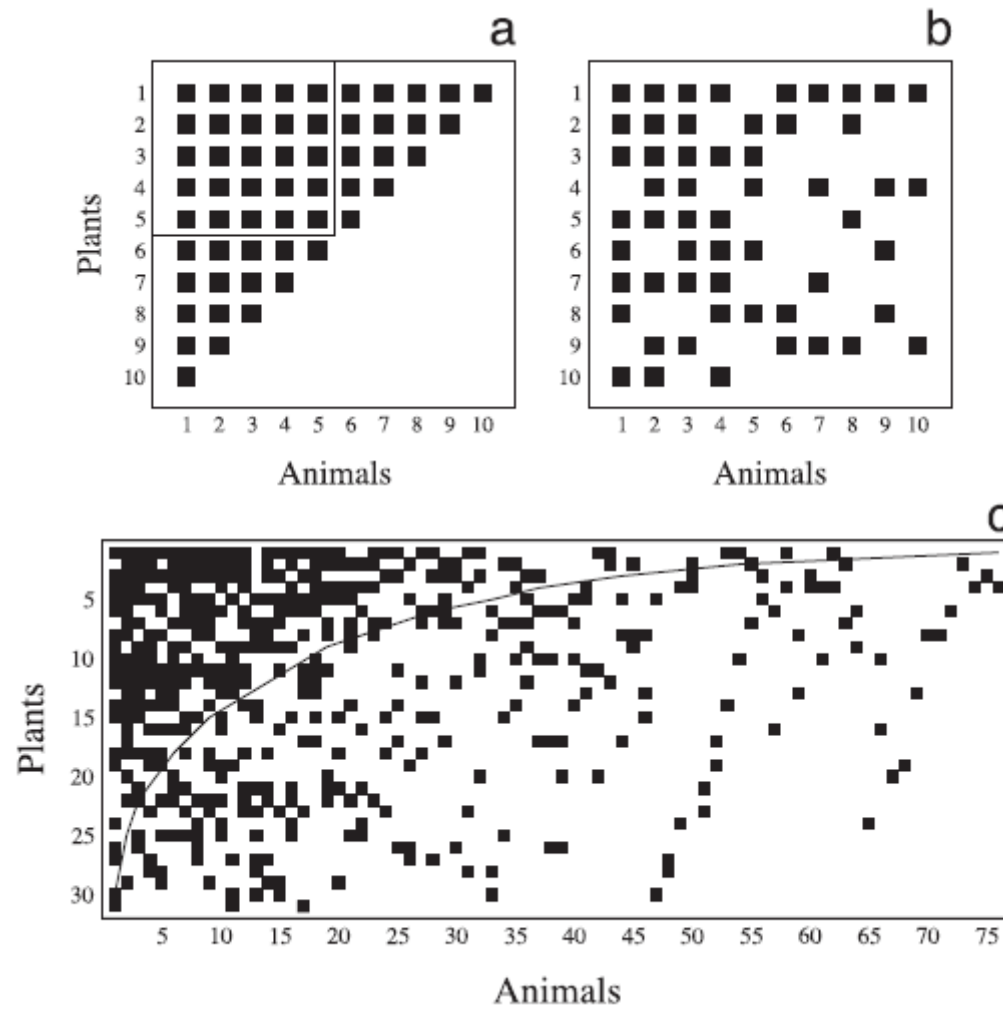


Figure 2 Cumulative distribution of connectivities (number of links per species, k , or degree) for different examples of the plant-animal interaction networks analysed (pollination and seed-dispersal mutualisms; Jordano 1987; Olesen & Jordano 2002). For these two-mode networks (see Fig. 1 for examples of the bipartite graphs) the distributions of links, $P(k)$, for the animal and plant species sets are given separately. Panels show the log-log plots of the cumulative distributions of species with 1, 2, 3, ..., k links (dots), power-law fits (solid lines) and truncated power-law fits (dotted lines). The distributions depart in most cases from the power-law beyond cut-off values, k_c .

Generalización 3. Muchas interacciones son débiles, pocas son fuertes



Generalización 4. Las redes mutualistas tienden a estar anidadas



Generalización 5. La mayoría de las interacciones son asimétricas

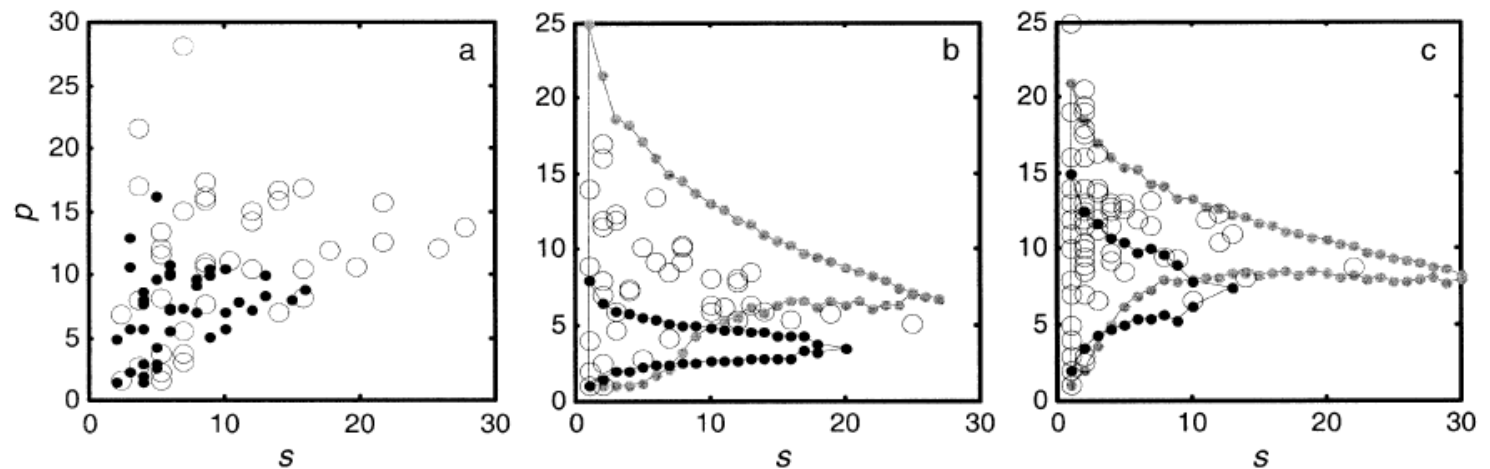
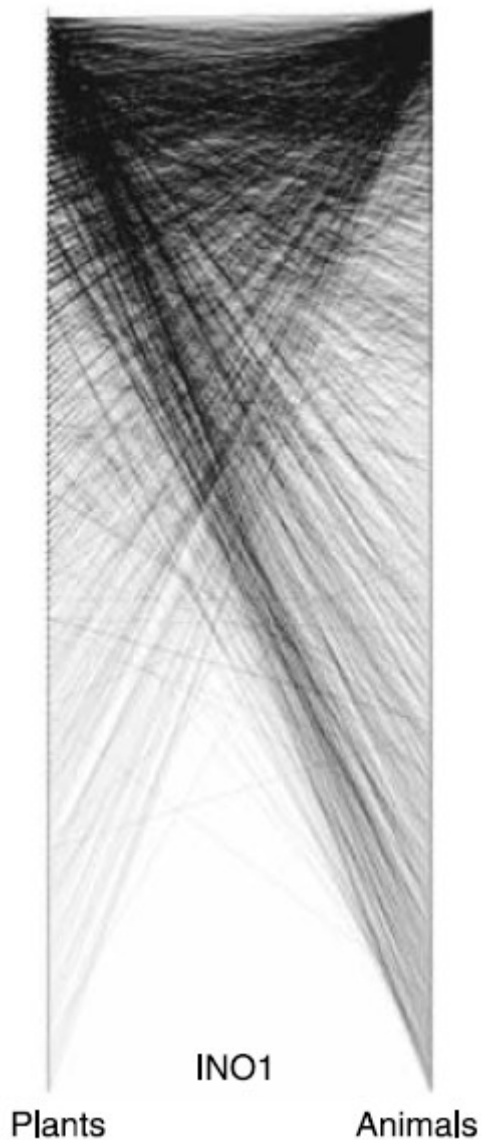


FIG. 1. Distribution of asymmetric specialization in plant–pollinator interaction networks. Plots show the average specialization of interaction partners (p) vs. the degree of specialization (s). (a) An example to illustrate the inability of the correlation coefficient to characterize asymmetric specialization. Heuristic data are shown for two communities with identical correlation coefficients ($r = 0.4265$), one with higher values of s and p (large open circles) than the other (black dots). Data for the Inouye and Pyke (1988) data set are shown for plants (b) and pollinators (c). Large open circles represent observed s - p values; black dots and line indicate the null space for model 1; gray dots and line indicate the null space for model 2. Notice that most extreme specialists (species with low values of s) do not have reciprocally specialized interaction partners (low values of p); a similar pattern was observed for all data sets (see Appendix B).

Vázquez & Aizen (2004) Ecology 85: 1251-1257

Generalización 5. La mayoría de las interacciones son asimétricas

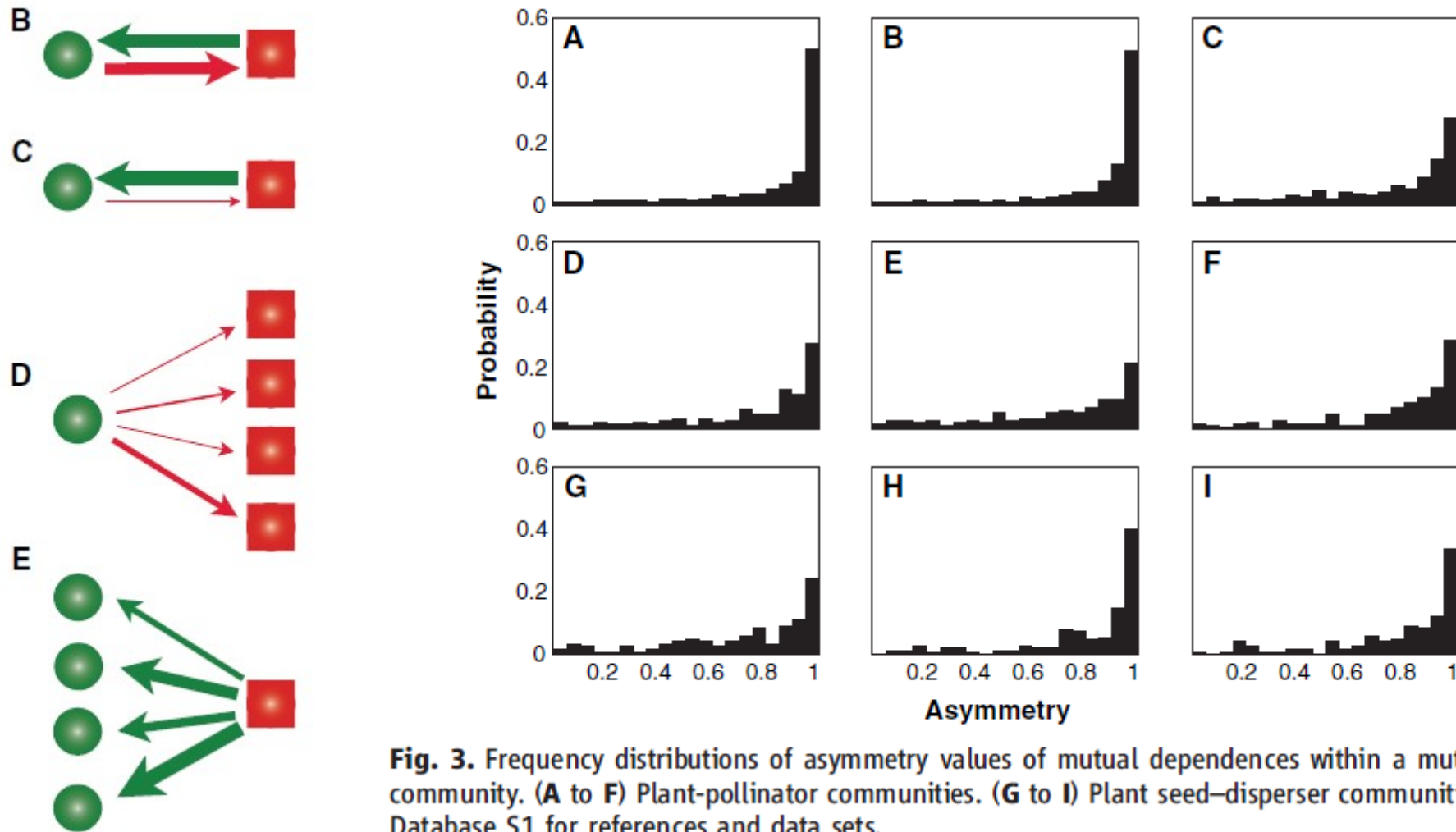
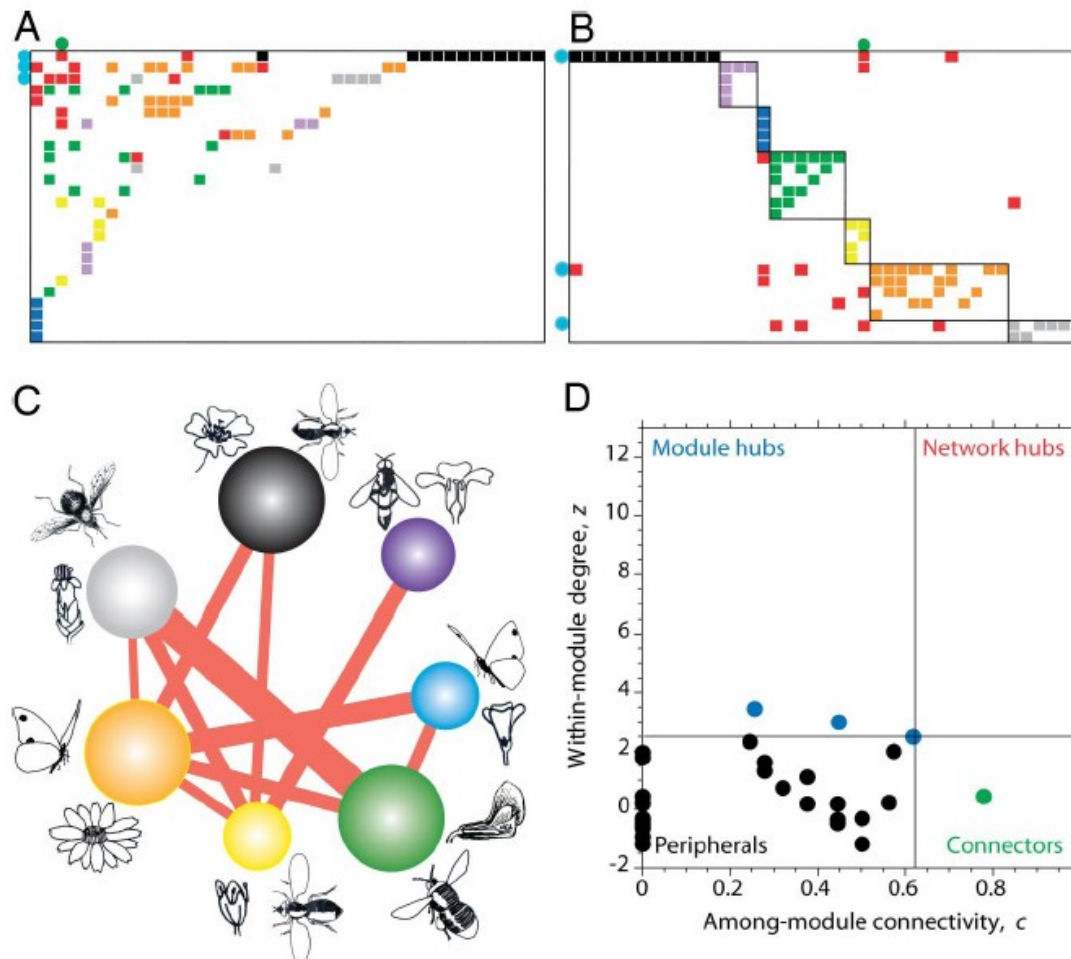


Fig. 3. Frequency distributions of asymmetry values of mutual dependences within a mutualistic community. (A to F) Plant-pollinator communities. (G to I) Plant seed-disperser communities. See Database S1 for references and data sets.

Bascompte et al. (2006) Science 312: 431-433

Generalización 6. Las redes mutualistas tienden a estar compartimentalizadas

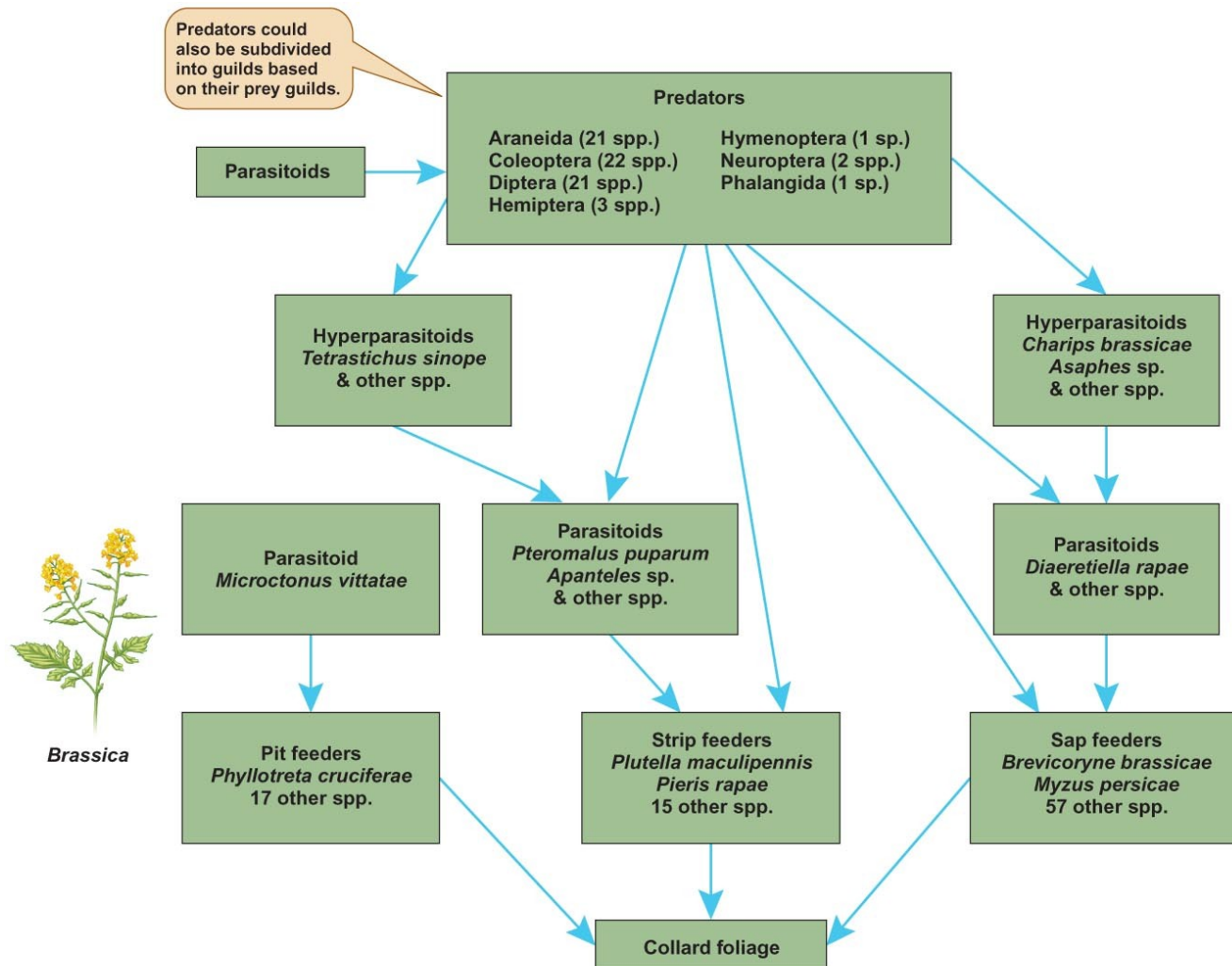


Olesen et al. (2007) PNAS 104: 19891-19896

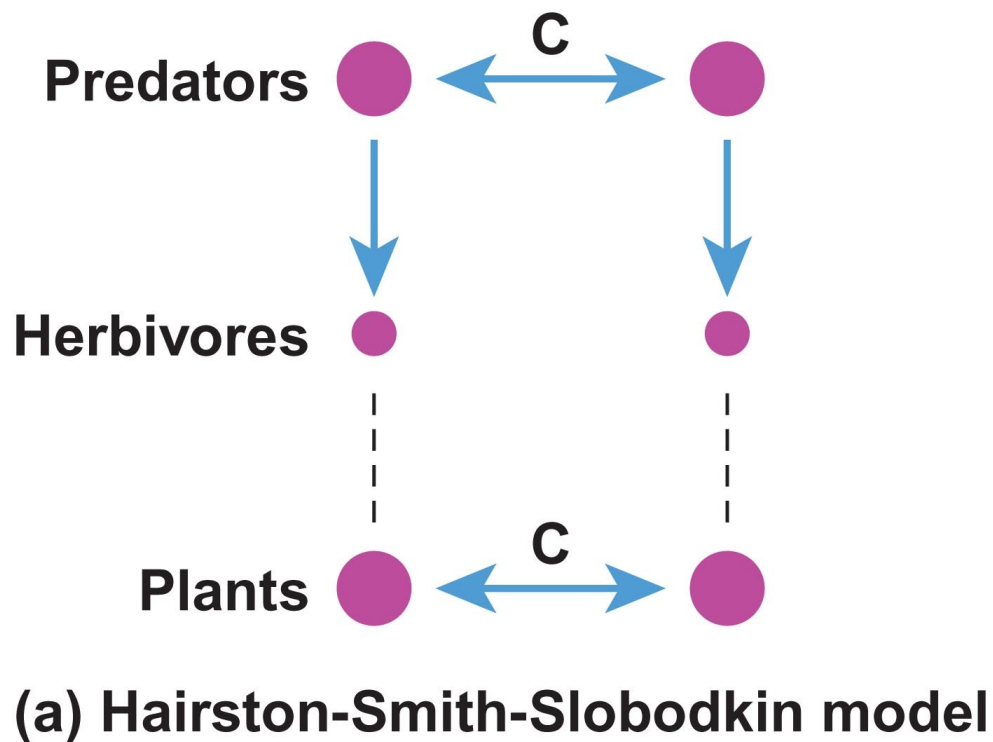
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Gremios: grupos de especies que pueden competir por recursos



Cascadas tróficas



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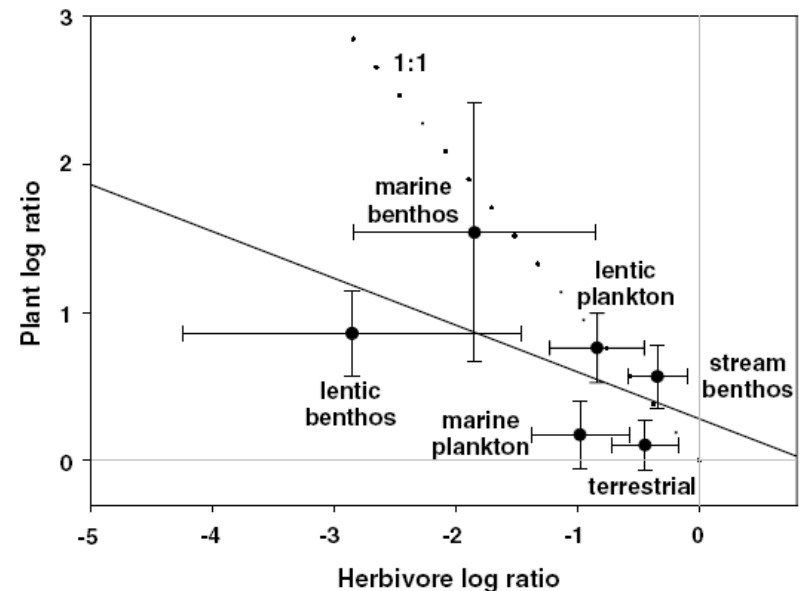
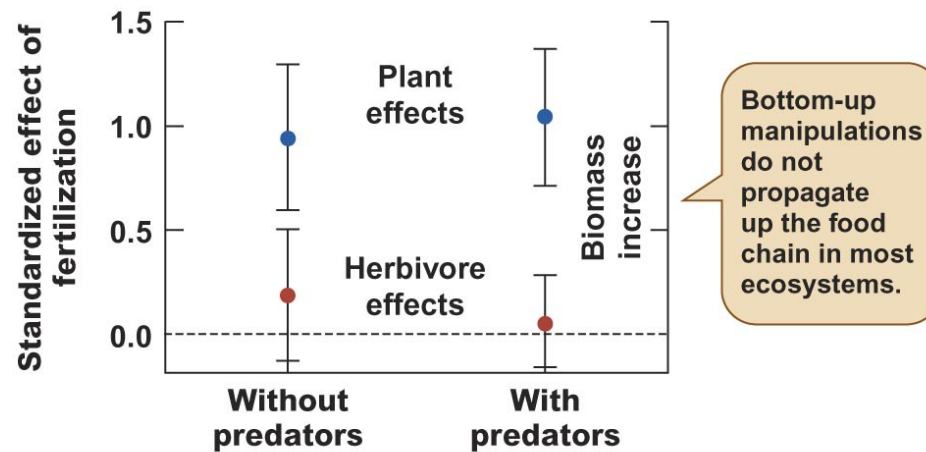
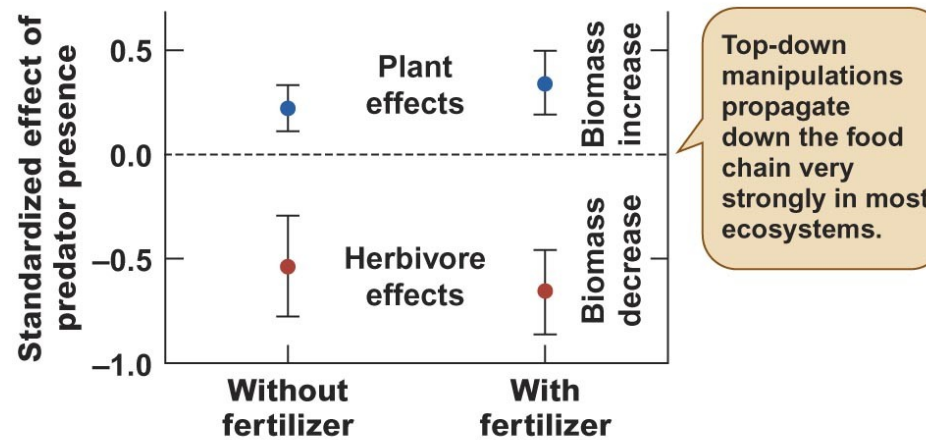


Figure 1 The effect size of predators ($\log_e$ ratio) on primary producers vs. herbivores in six ecosystems. Error bars are 95% confidence intervals. The effect of predators is significant if the confidence interval does not overlap zero (the grey lines). There were significant differences among systems in both plant and herbivore responses (plants: one-way ANOVA, $F = 7.70$, d.f. = 5, $P < 0.0001$, $R^2 = 0.29$; herbivores: $F = 10.34$, d.f. = 5, $P < 0.0001$, $R^2 = 0.35$). The equation for the linear regression relating the plant and herbivore effect sizes (the solid line) is $Y = 0.28 - 0.32x$ ($n = 6$, one-tailed $P = 0.11$, $R^2 = 0.34$). The dotted line shows the 1 : 1 relationship.

Cascadas tróficas



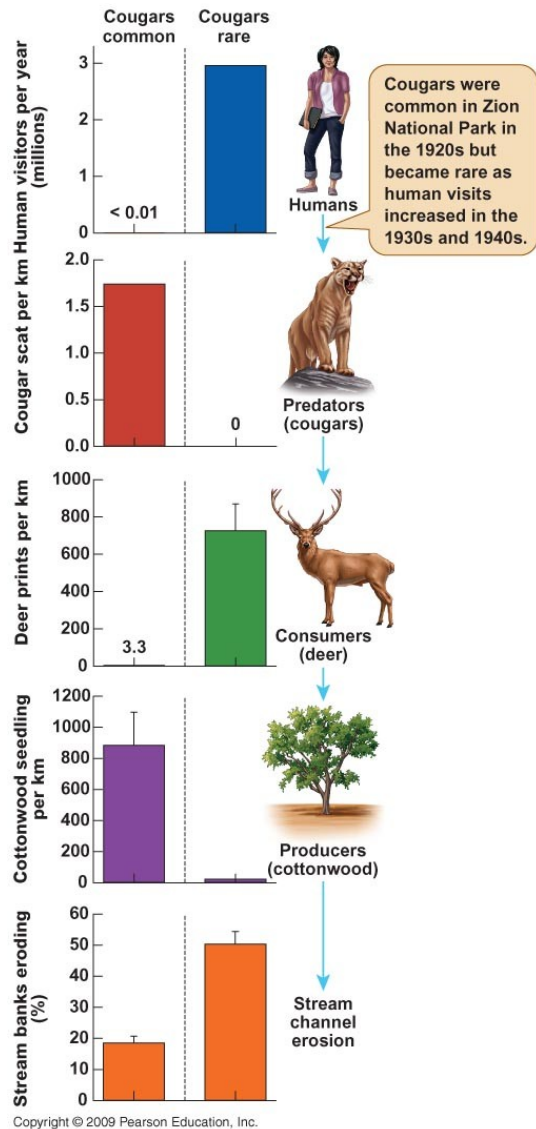
(a) Bottom-up manipulations



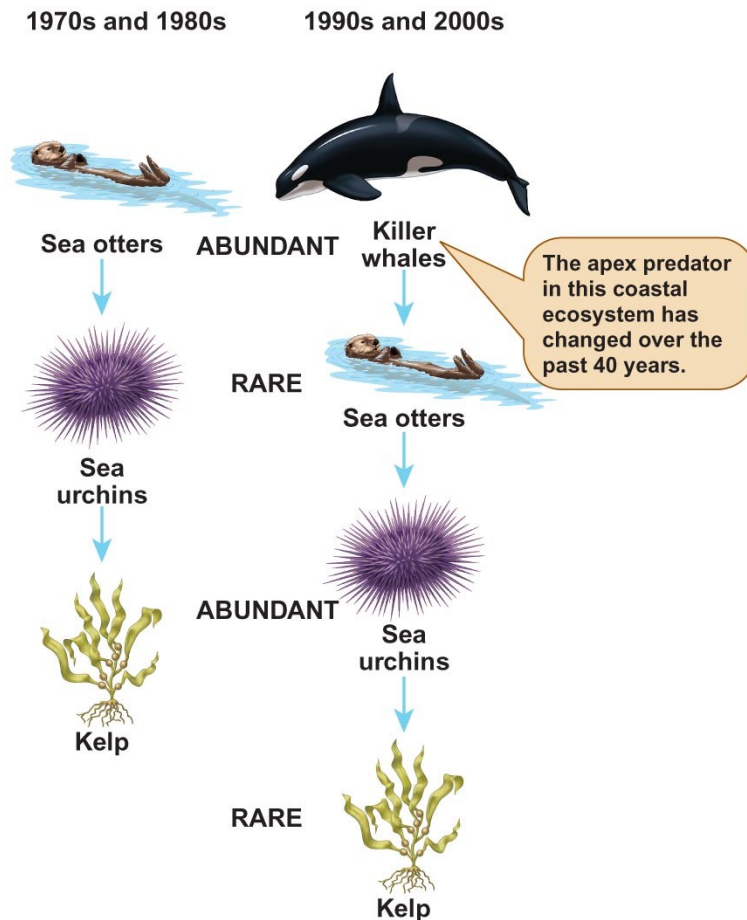
(b) Top-down manipulations

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Cascadas tróficas



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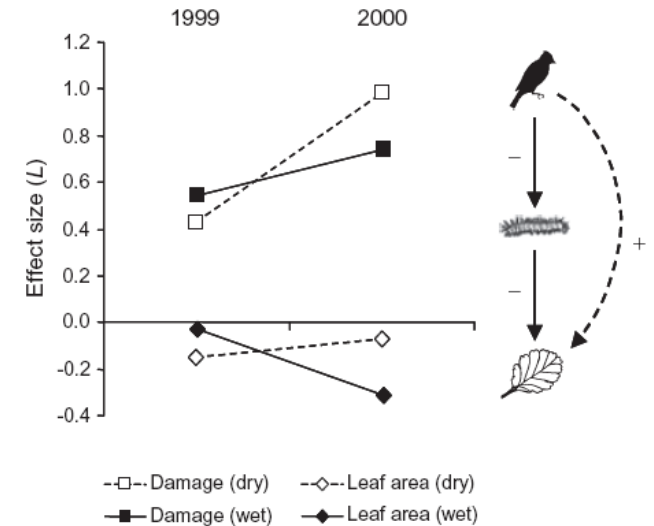


Fig. 3. The magnitude of bird exclusion effects on leaf-chewer damage (squares) and mean leaf size (diamonds) of *Nothofagus pumilio* saplings in dry and wet forest sites. Effect sizes were estimated using the log response ratio, $L = \ln (X_E / X_C)$. Positive values indicate that bird exclusion increased leaf damage, whereas negative values indicate that exclosures reduced mean leaf size (including both insect damaged and intact leaves). The diagram shows the direct (solid arrows) and indirect (dashed arrow) effects involved in the trophic cascade; birds were assumed to decrease either the abundance or activity of leaf-chewing insects.

Fuente: Mazía et al.
(2009) Austral Ecol. 34:
359-367

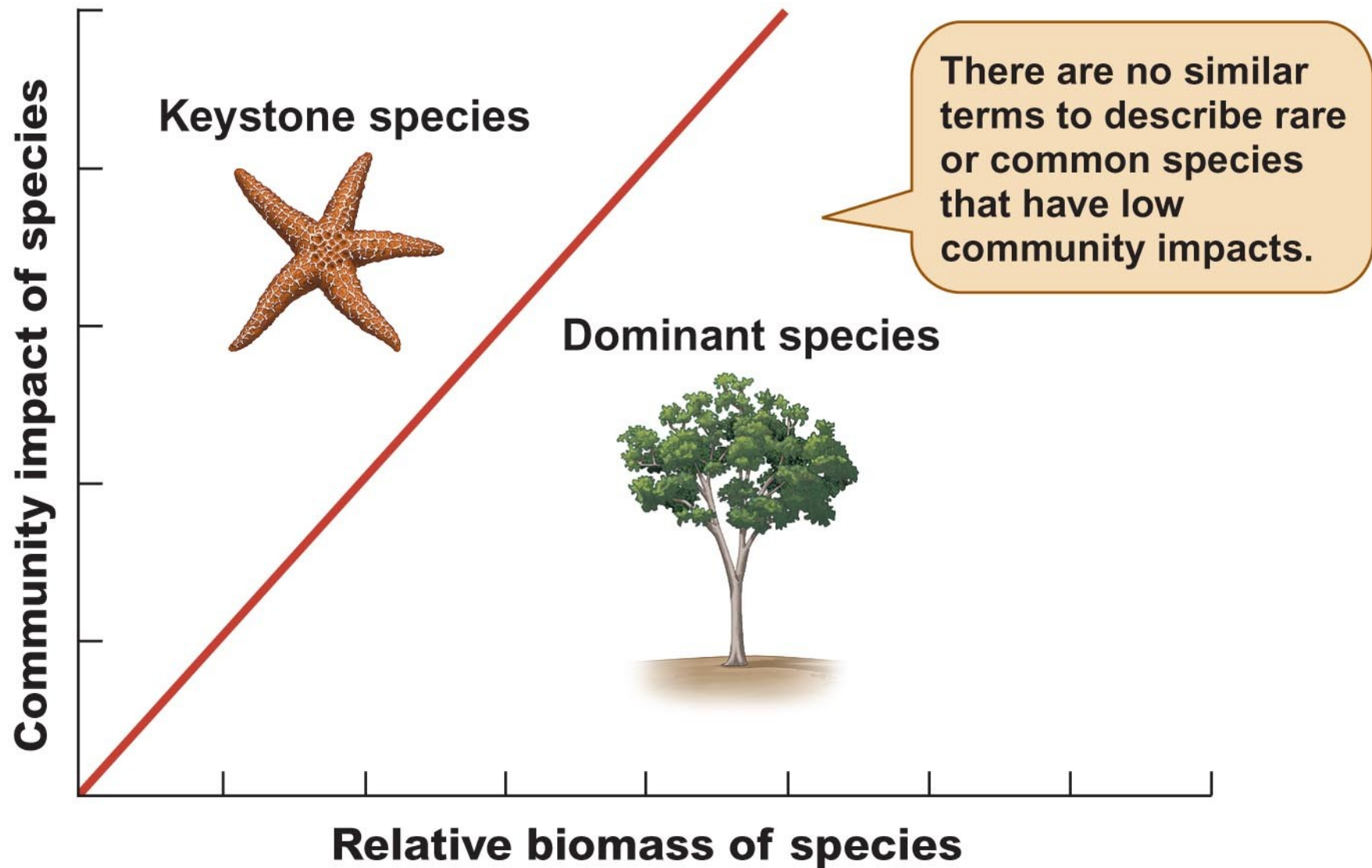
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Importancia de las especies

- Especies clave: sus actividades determinan la estructura comunitaria, su impacto es grande relativo a su abundancia
- Especies dominantes: son las más importantes en abundancia o biomasa

Species clave vs. dominantes



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Especies clave

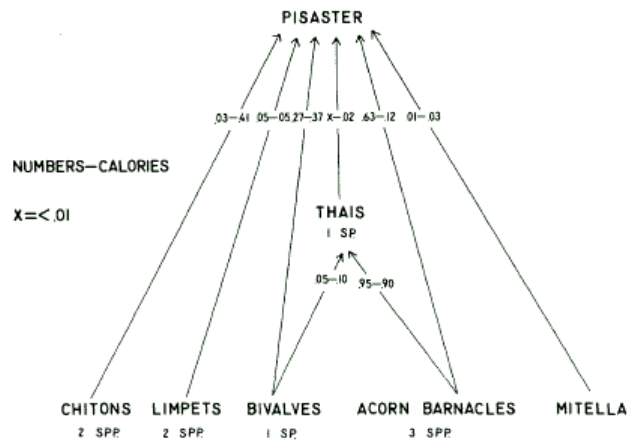
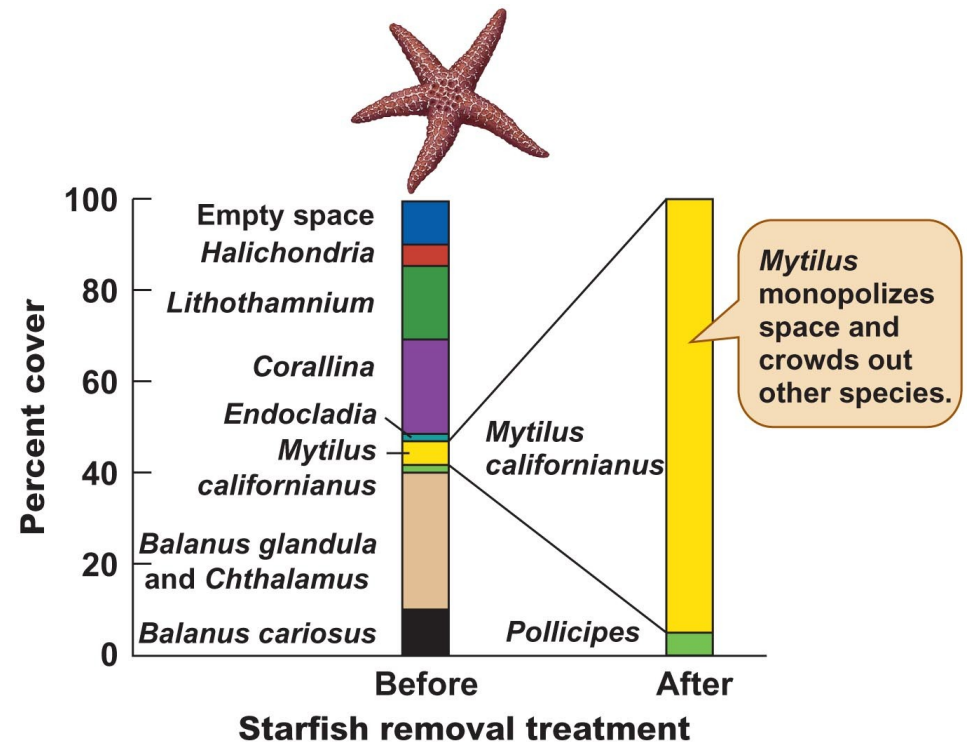


FIG. 1. The feeding relationships by numbers and calories of the *Pisaster* dominated subweb at Mukkaw Bay. *Pisaster*, N = 1049; *Thais*, N = 287. N is the number of food items observed eaten by the predators. The specific composition of each predator's diet is given as a pair of fractions; numbers on the left, calories on the right.

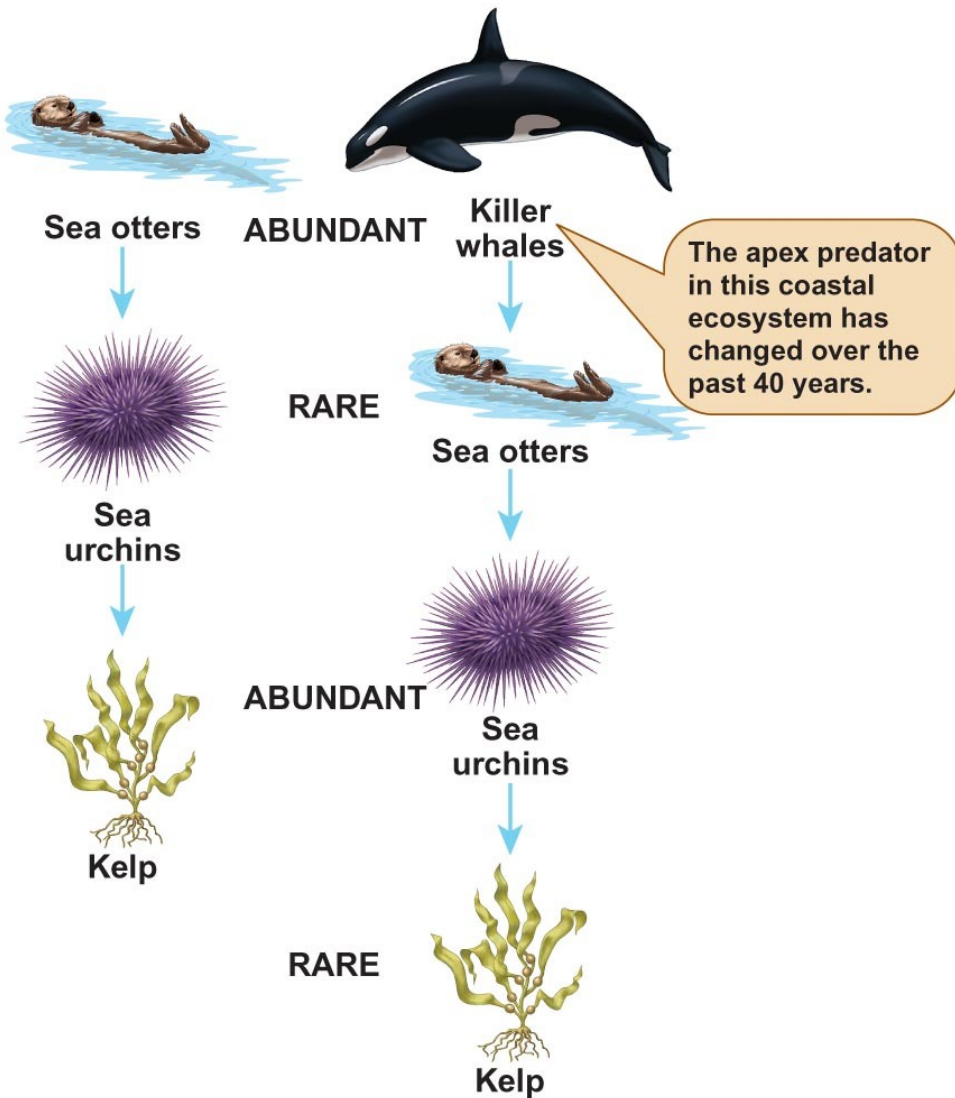


Fuente: Paine (1966) Am. Nat. 100: 65-75

Especies clave

1970s and 1980s

1990s and 2000s



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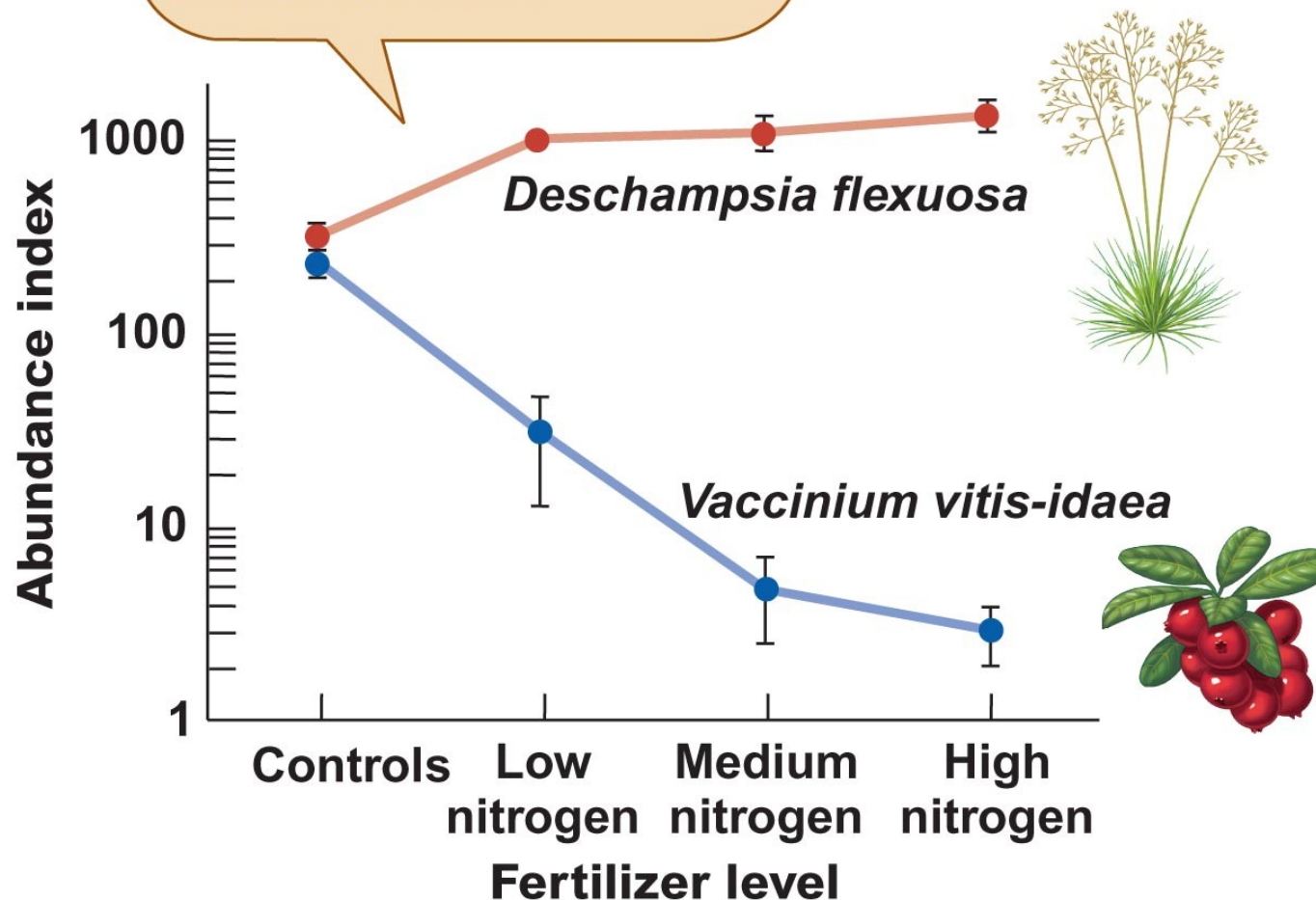
Especies dominantes



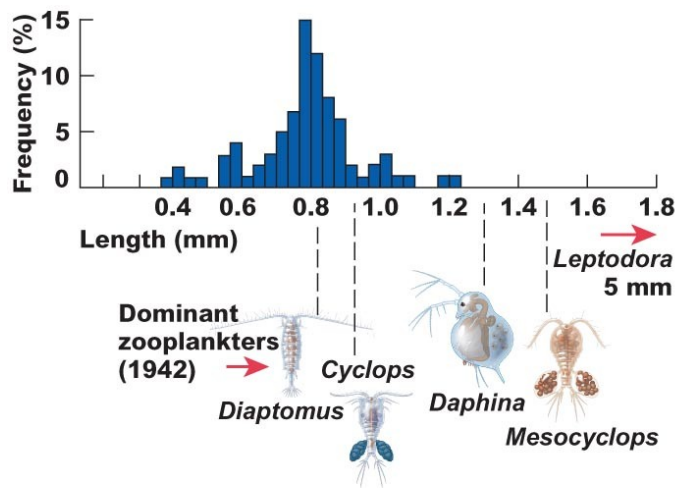
Jarilla (*Larrea divaricata*) en Villavicencio

Cambio en la dominancia con la adición de nutrientes

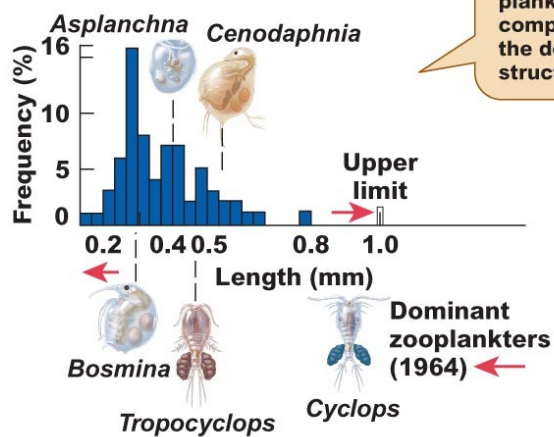
Dominance in these boreal forest plant communities can be completely changed by nutrient additions.



Cambio en la dominancia con la depredación



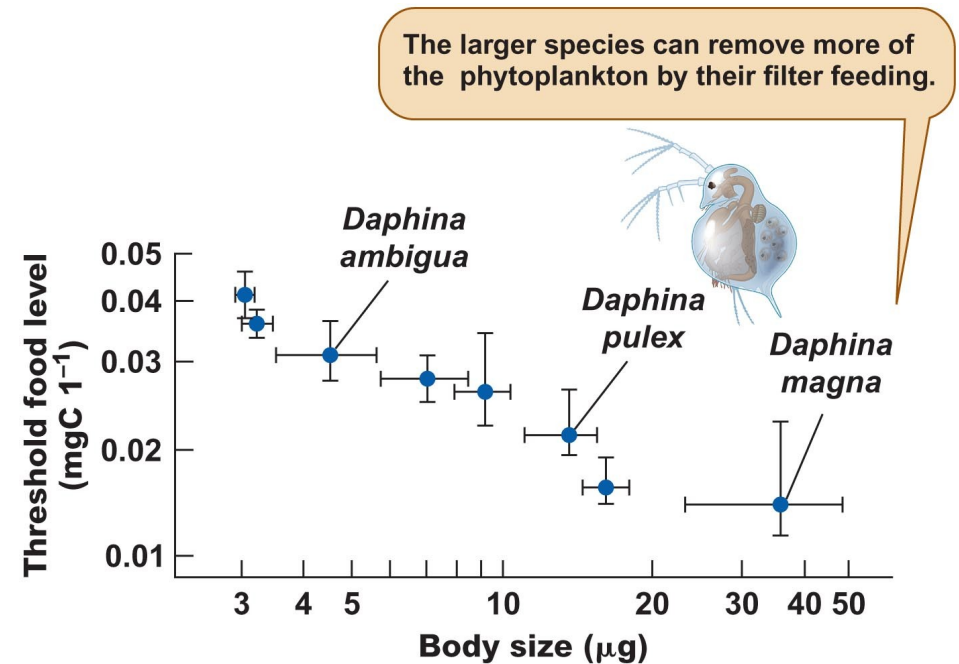
(a) 1942 no *Alosa*



(b) 1964 with *Alosa*

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The introduction of a planktivorous fish completely changed the dominance structure of this lake.

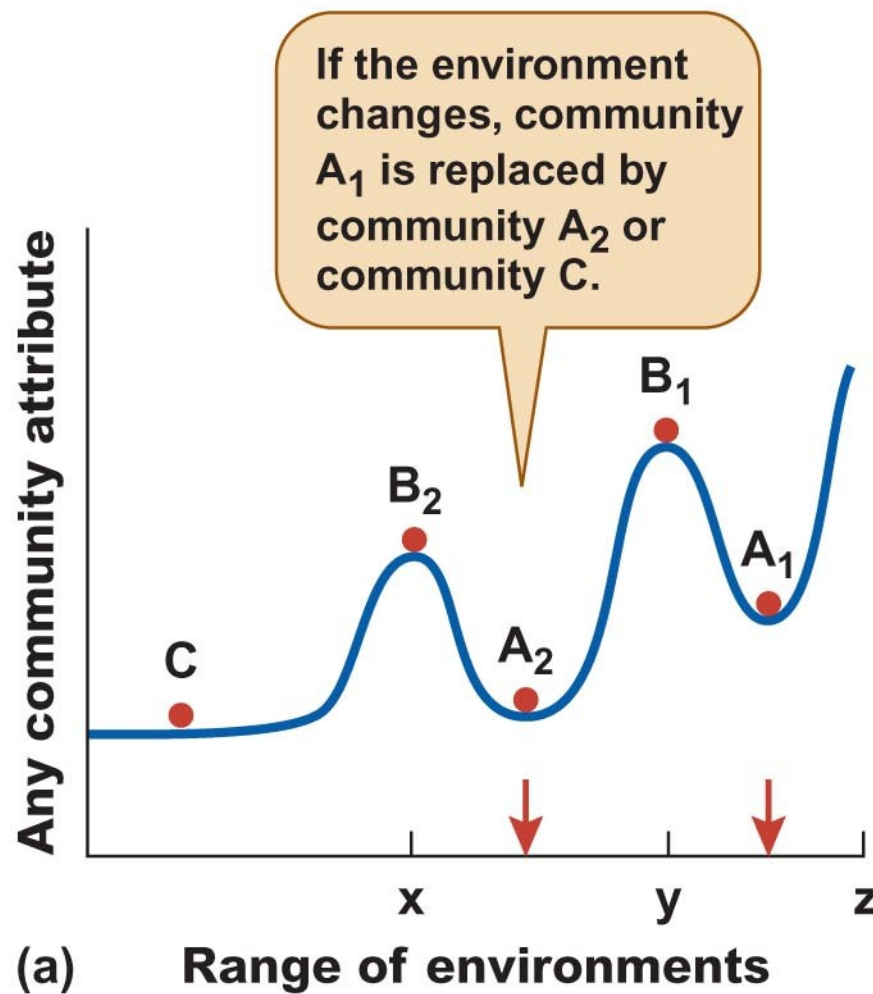


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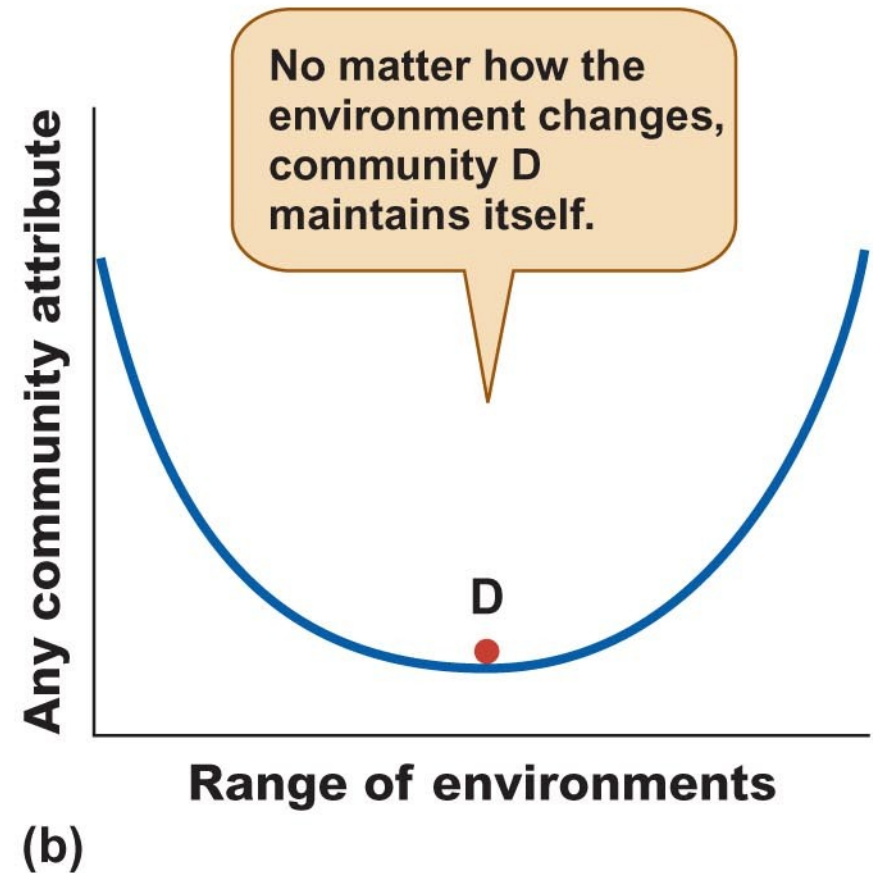
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Tipos de estabilidad



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Tipos de estabilidad

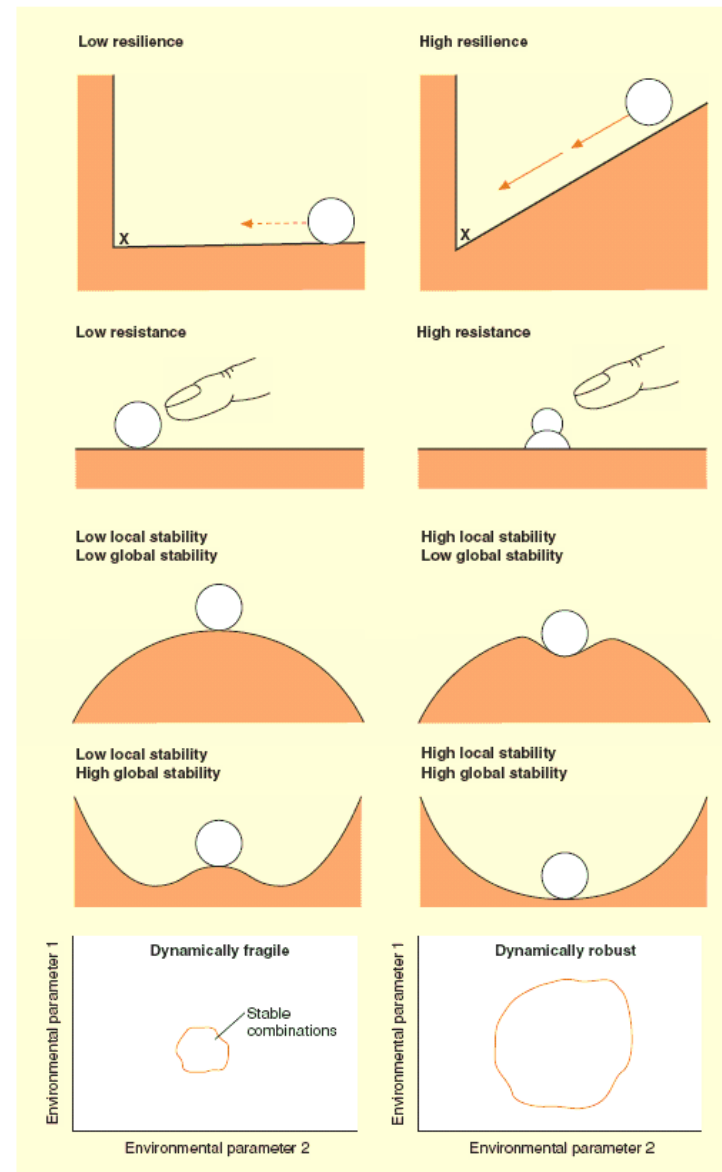
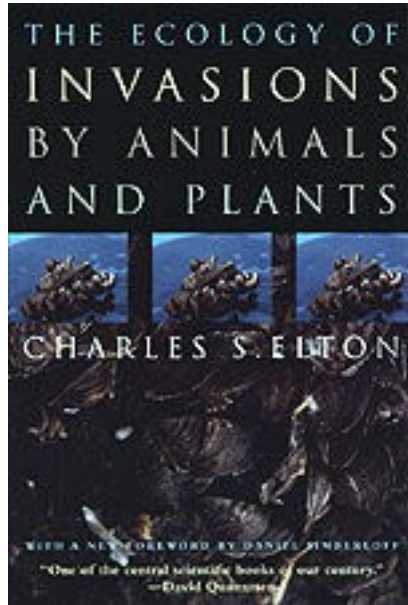


Figure 20.7 Various aspects of stability, used in this chapter to describe communities, illustrated here in a figurative way. In the resilience diagrams, X marks the spot from which the community has been displaced.

Ideas sobre estabilidad comunitaria

- MacArthur (1955) y Elton (1958): Más especies más estabilidad
- May (1972): Más especies *menos* estabilidad en ecosistemas “teóricos”
- Yodzis (1981) y otros: Los ecosistemas reales son estables a pesar de su riqueza
- McCann et al. (1998): Las interacciones débiles estabilizan las redes tróficas

Elton: complejidad = estabilidad



“El balance de comunidades simples de plantas y animales es más fácilmente alterado que el de las más complejas; es decir, más sujeto a oscilaciones destructivas en poblaciones, y más vulnerable a las invasiones.”

C. S. Elton (1958: 145) *The Ecology of Invasions by Plants and Animals*

MacArthur y Watt: complejidad = estabilidad

MacArthur (1955): mayor número de presas mayor estabilidad poblacional

Watt (1964): mayor número de presas menor estabilidad poblacional

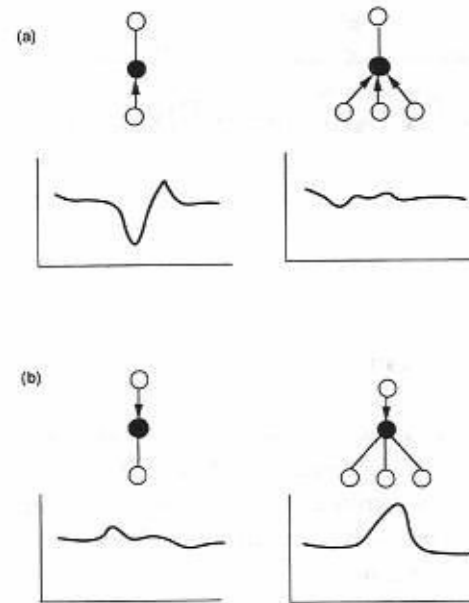


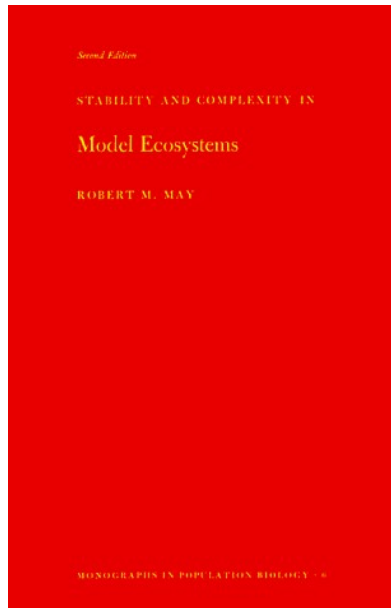
Figure 4.1. Two opposing arguments for the possible relationships between population variability and the degree of polyphagy: (a) MacArthur's suggestion that monophagous species (left) should be more variable than polyphagous species (right) because they will decrease most when one prey species declines in abundance and (b) Watt's contrasting argument that polyphagous species may be more variable because they may be able to reach higher numbers during periods when their predators fail to control their densities. Circles represent species, and lines represent trophic interactions between species, such that species higher on the page feed on species beneath them. The species for which we measure the population variability is shaded. Arrows indicate which trophic interactions are most important in determining the density of the species of interest.

May: complejidad = inestabilidad

$s(mC)^{1/2} < 1$: estabilidad

$s(mC)^{1/2} > 1$: inestabilidad

“The central point remains that, if we contrast simple few-species mathematical models with the analogously simple multispecies models, the latter are in general less stable.”



R. M. May (1974) *Stability and Complexity in Model Ecosystems*. Princeton

Ecología: Teórica

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Pimm y Lawton (y varios más): complejidad = inestabilidad

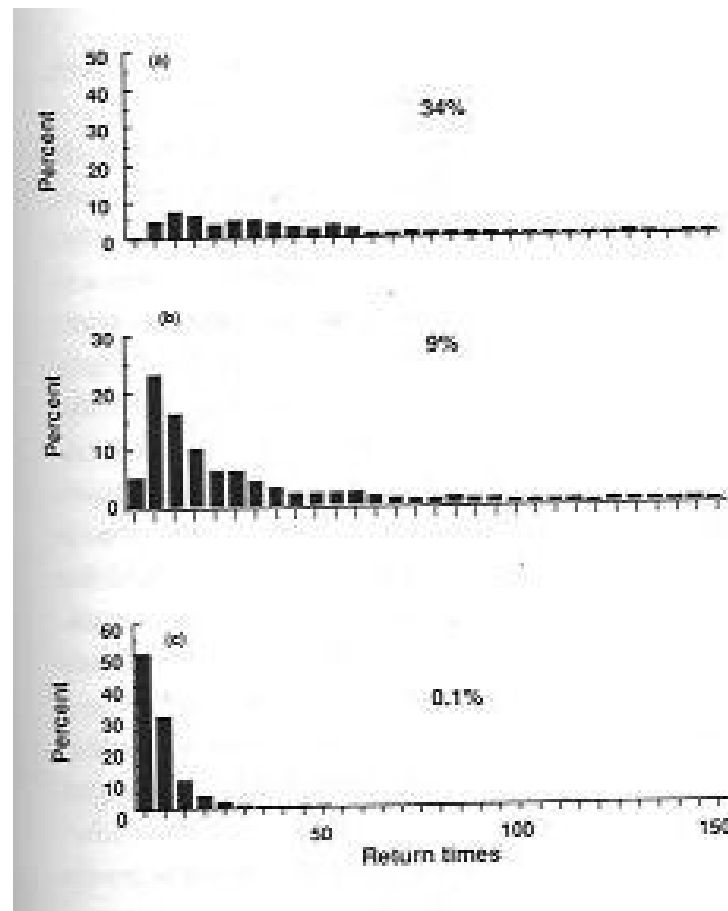


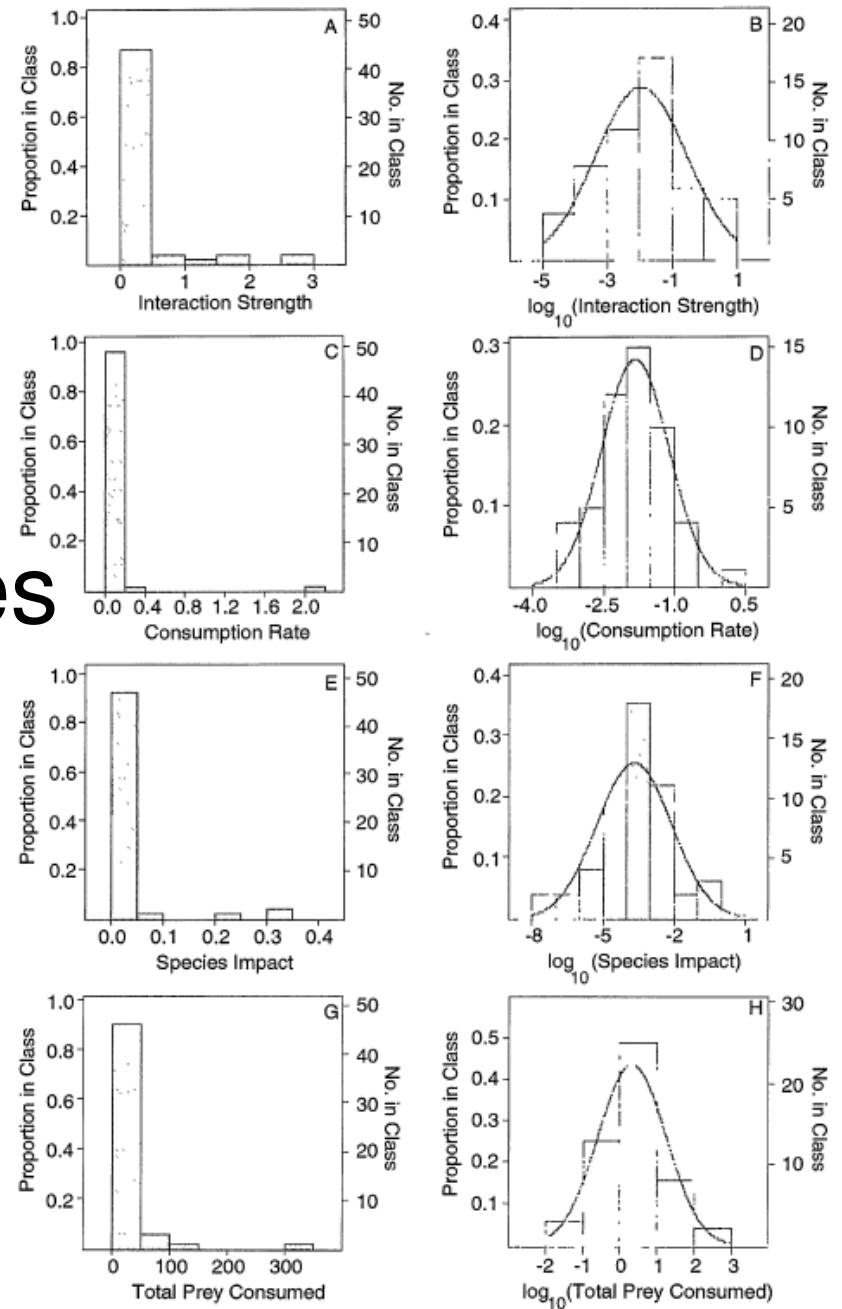
Figure 2.6. Distribution of return times from nearly two thousand models of three food-web configurations: (a), four trophic levels, one species per level; (b), three trophic levels, with two species at the lowest trophic level; and (c) two trophic levels, with three species at the lower trophic level. The number on each part of the figure represents the percentage of models with return times in excess of 150 time units. (The time units are arbitrary and are those used to quantify the rates of change of the species densities.) The return times were calculated as the reciprocals of the largest eigenvalue of each model's interaction matrix; for details, see appendix equation (A2). (Redrawn from Pimm and Lawton 1977.)

Yodzis: preguntemos a la madre naturaleza...

“Encuentro que la estabilidad (en el sentido de una tendencia a volver al supuesto equilibrio luego de una perturbación pequeña) es mucho más probable si las fuerzas de interacción son elegidas según la naturaleza de los organismos que componen cada red trófica y no en forma estrictamente aleatoria.”

P. Yodzis (1981) *Nature* 289: 674-676

En la naturaleza, muchas interacciones son débiles y pocas fuertes, y eso estabiliza a las comunidades



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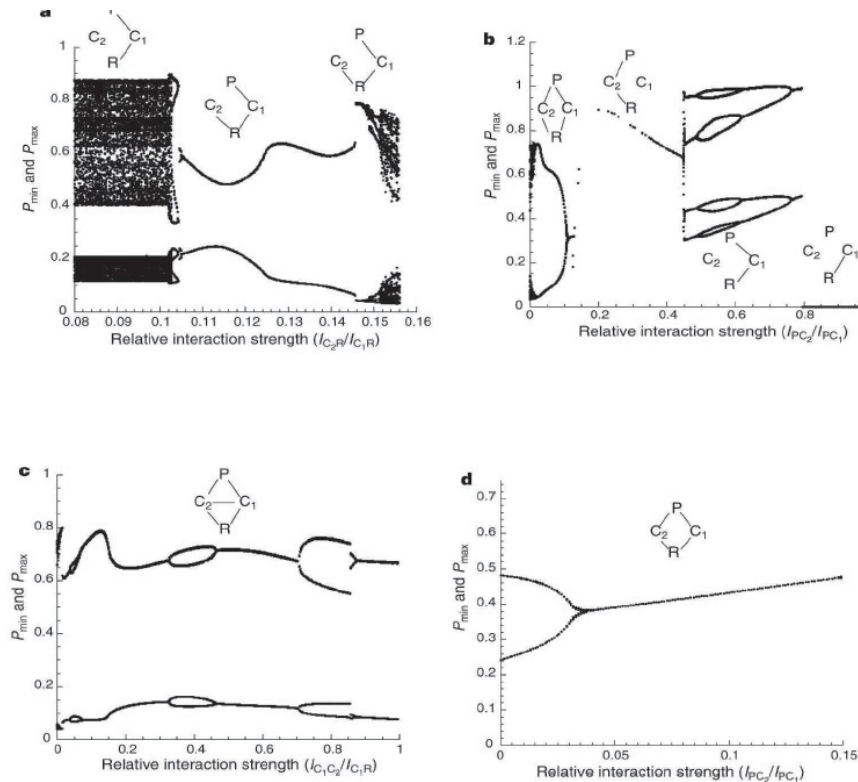
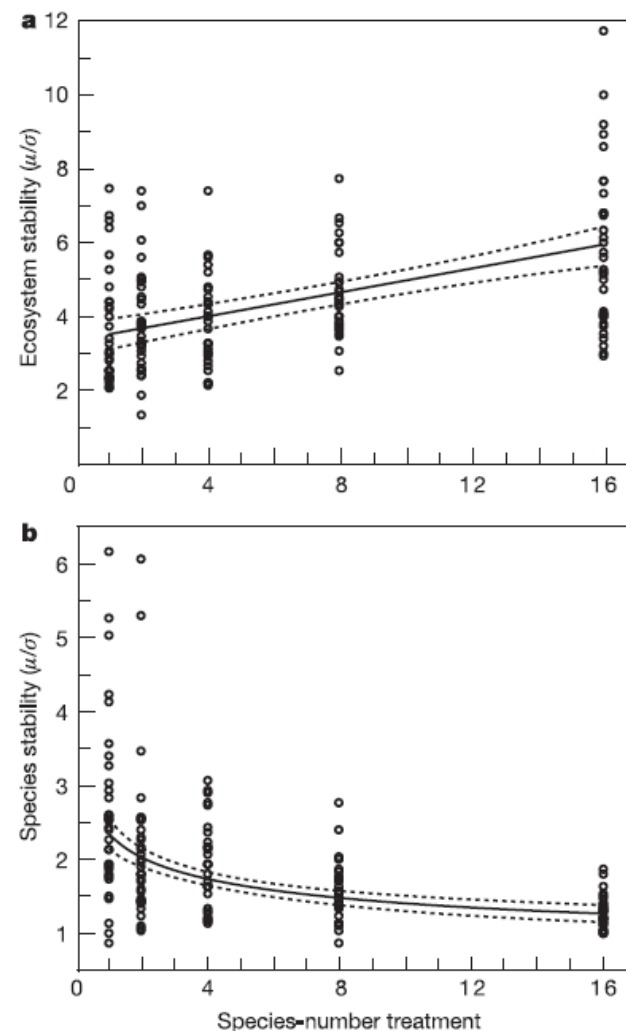


Figure 2 The local minima and maxima for top predator density, P , attained in the attracting solutions for a range of relative interaction strengths. Food-web configurations are given as a function of the relative interaction strengths. Food-web configurations are given as a function of the relative interaction strength.

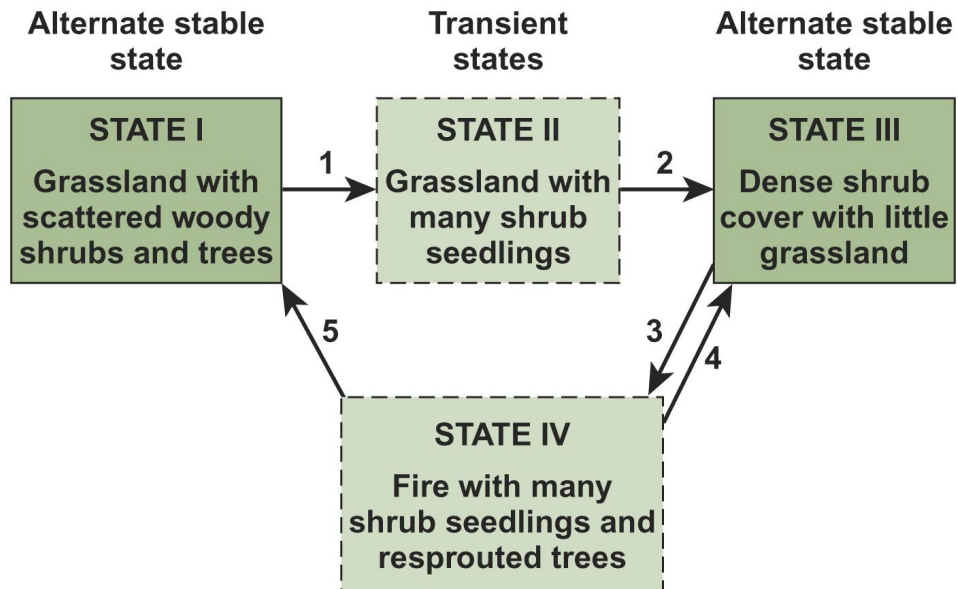
Whenever the configuration lacks an explicit link between a species and the rest of the connected web this implies that the species cannot persist. a, Exploitative competition. b, Apparent competition. c, Intraguild predation. d, The configuration used in b, starting with a limit cycle solution ($l_{C_2R}/l_{C_1R} \approx 0.62$).

Estabilidad comunitaria

Figure 1 | Dependence of temporal stability of each plot on experimentally imposed species-number treatment. **a**, Ecosystem temporal stability for the decade from 1996 to 2005 was an increasing function of the number of planted species. Ecosystem stability is the ratio of mean plot total biomass to its temporal standard deviation, determined after detrending. The regression line and its 95% confidence interval are shown (untransformed data: $F_{1,159} = 43.7$, $P < 0.0001$). To reduce the difference in y axis scale between the two parts of this figure, a single data point (species number of 16, ecosystem stability of 15.76) is not shown but was included in all analyses. **b**, Plot-average species temporal stability, determined with species biomass data for 2001–2005, was a declining function of the number of planted species. The regression curve and 95% confidence intervals are based on a fit of $\log(\text{species stability})$ on $\log(\text{species number})$, with $F_{1,159} = 72.3$, $P < 0.0001$.



Estados múltiples alternativos



(a)



(b)

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Estados múltiples alternativos

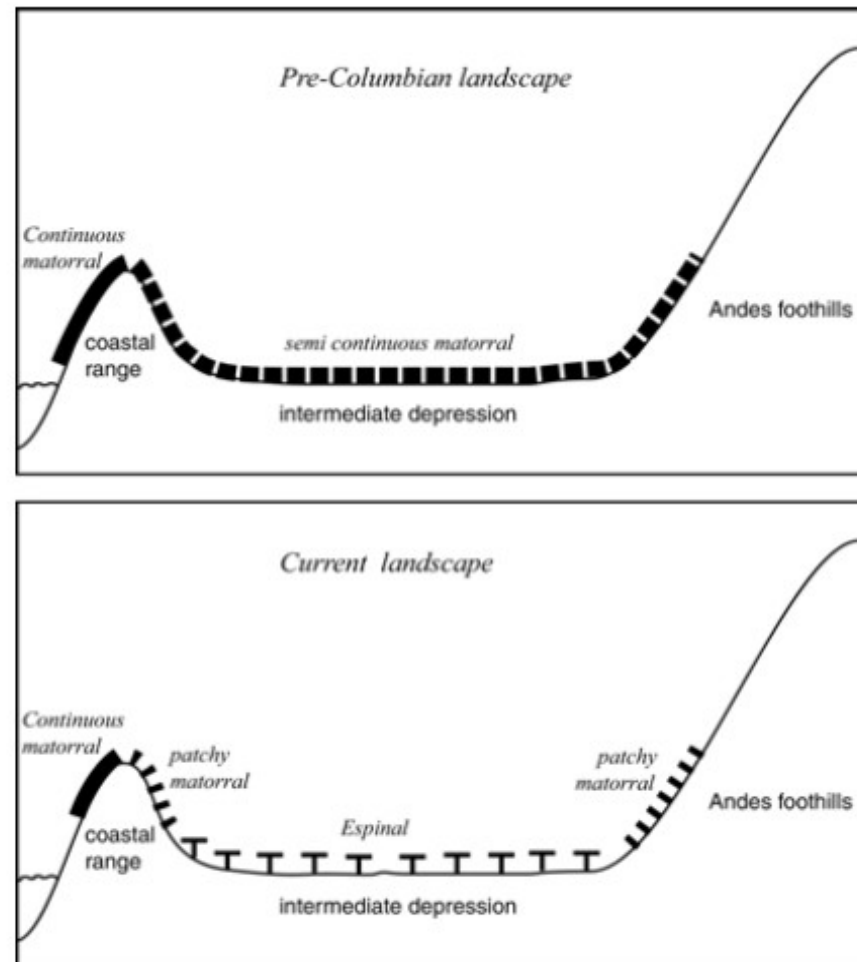


Figure 1. Schematic representation of the pre-Columbian (upper panel) and the current (lower panel) distribution of dominant vegetation structures in the central Chilean landscape.

Estados múltiples alternativos

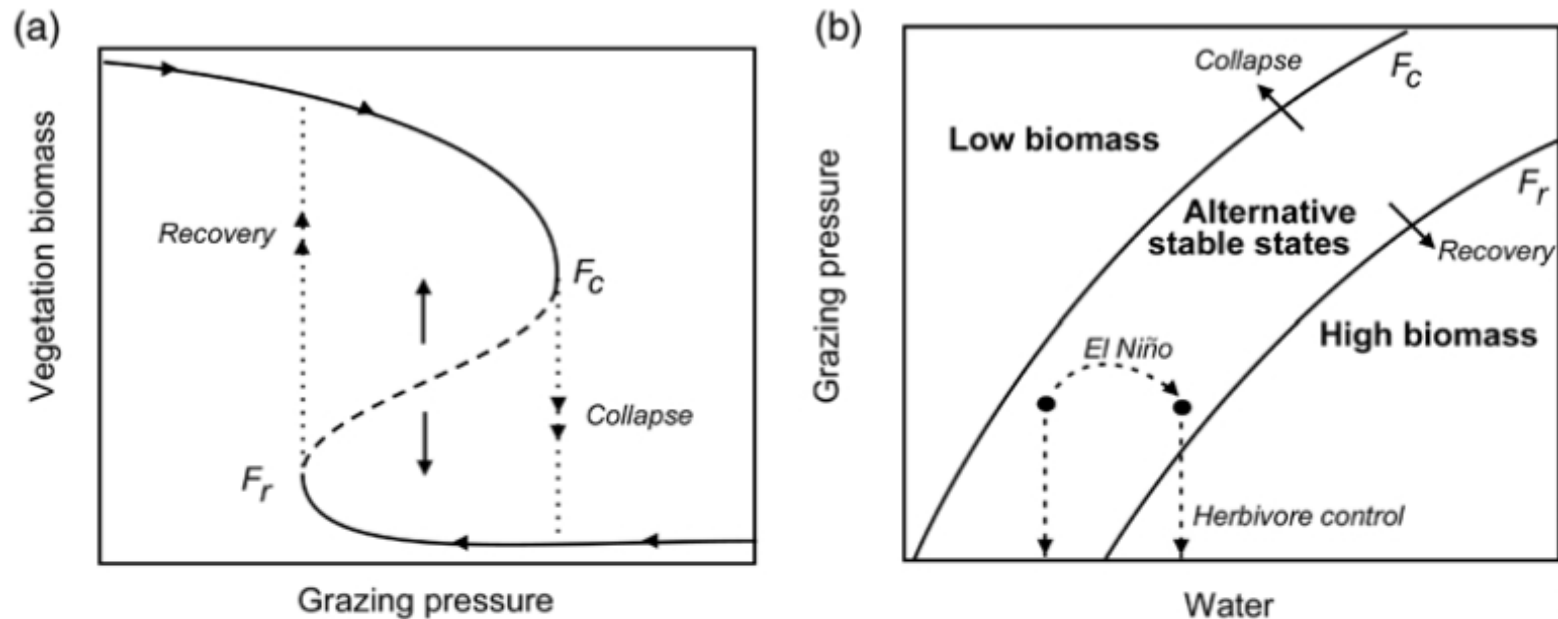
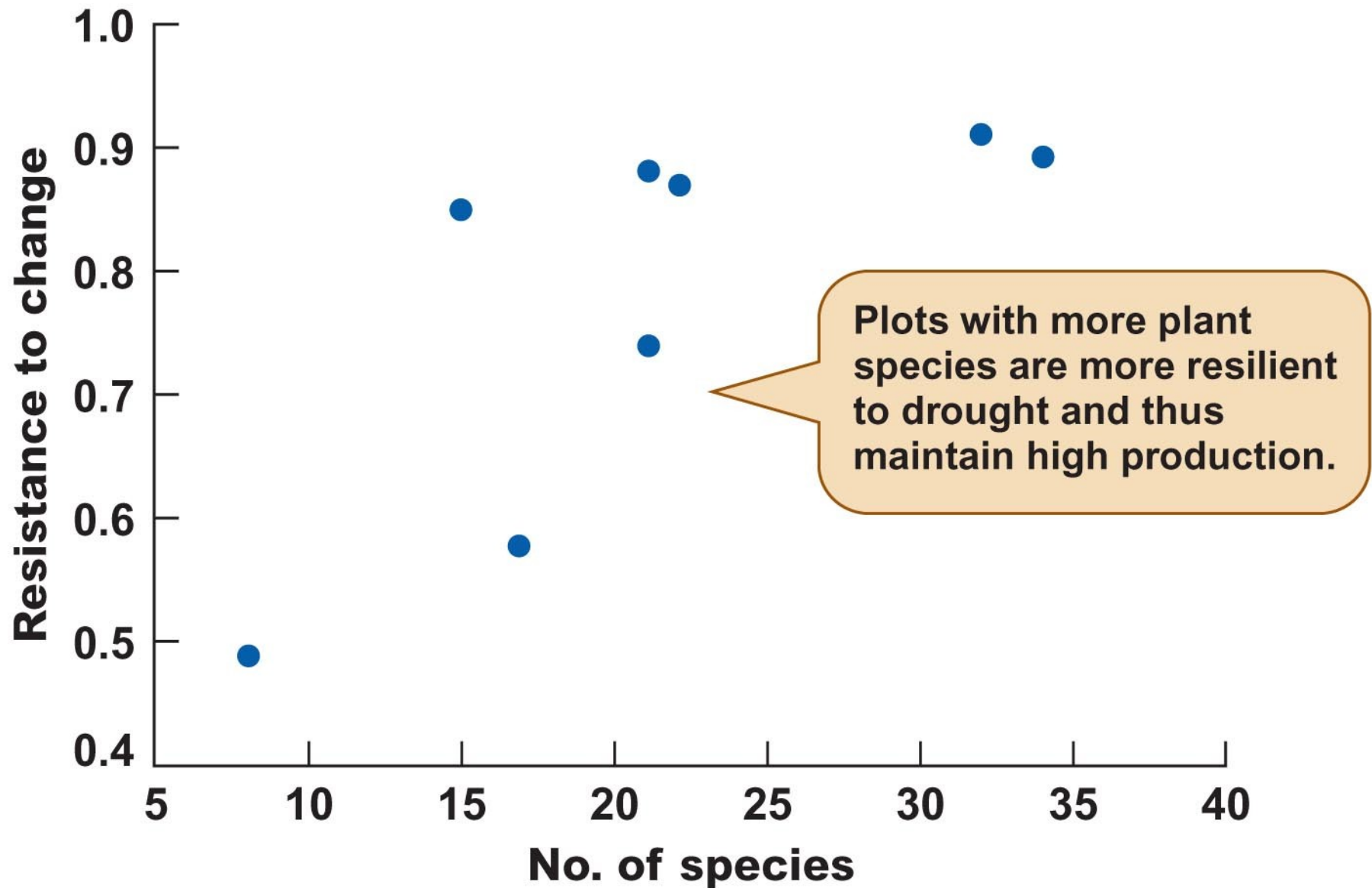


Figure 2. The response of semi-arid vegetation to increased grazing pressure may be discontinuous due to the presence of alternative stable states (panel a). In the absence of grazing vegetation, biomass is relatively high. The effect of a gradual increase in grazing is minor until a critical threshold (F_c) is reached, at which time the vegetation biomass collapses to a low level. Recovery from this state is difficult because the low-biomass state and the high-biomass state (upper and the lower branches of the curve) represent alternative attractors for intermediate grazing pressures. Only when grazing pressure is reduced below another low critical level (F_r) does the high-biomass state recover. To see how effects of grazing and water availability may interact, the position of the two bifurcation points (F_c and F_r) is plotted as a function of water availability (panel b). Under drier conditions, critical grazing rates for collapse (F_c) and for recovery (F_r) of vegetation are assumed to be lower. An implication is that not only a reduction in grazing pressure, but also a rainy El Niño event may potentially trigger vegetation recovery provided that it enhances water availability sufficiently to pass the critical level (F_r). The dotted arrows illustrate that exclusion of herbivores coinciding with an increase in water availability due to an El Niño event may bring the system over the critical threshold to induce vegetation recovery, even if those two factors by themselves would be insufficient to trigger the switch. (Reproduced, with permission, from Holmgren and Scheffer 2001, © Springer-Verlag.)

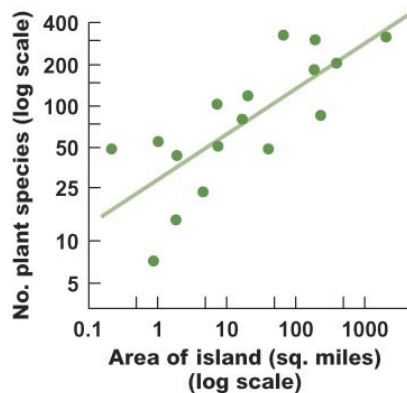
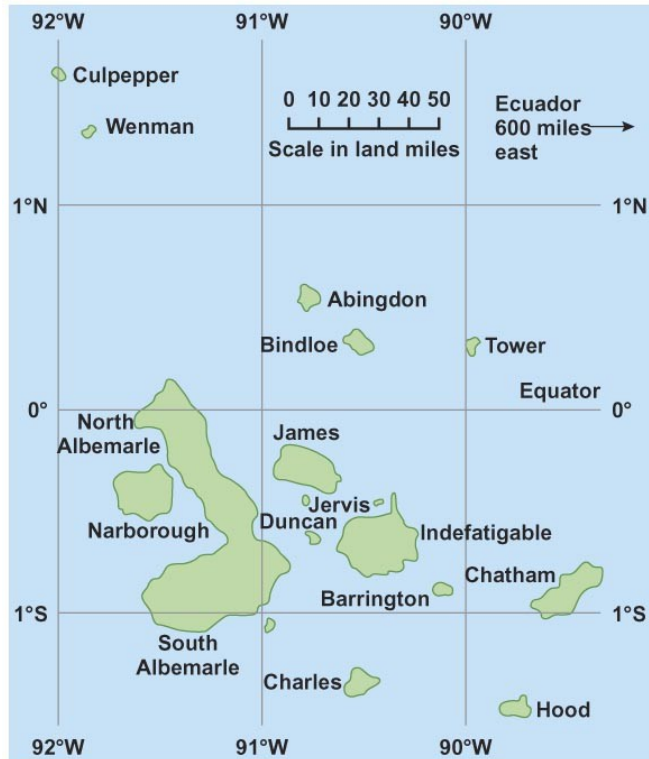
Estabilidad comunitaria



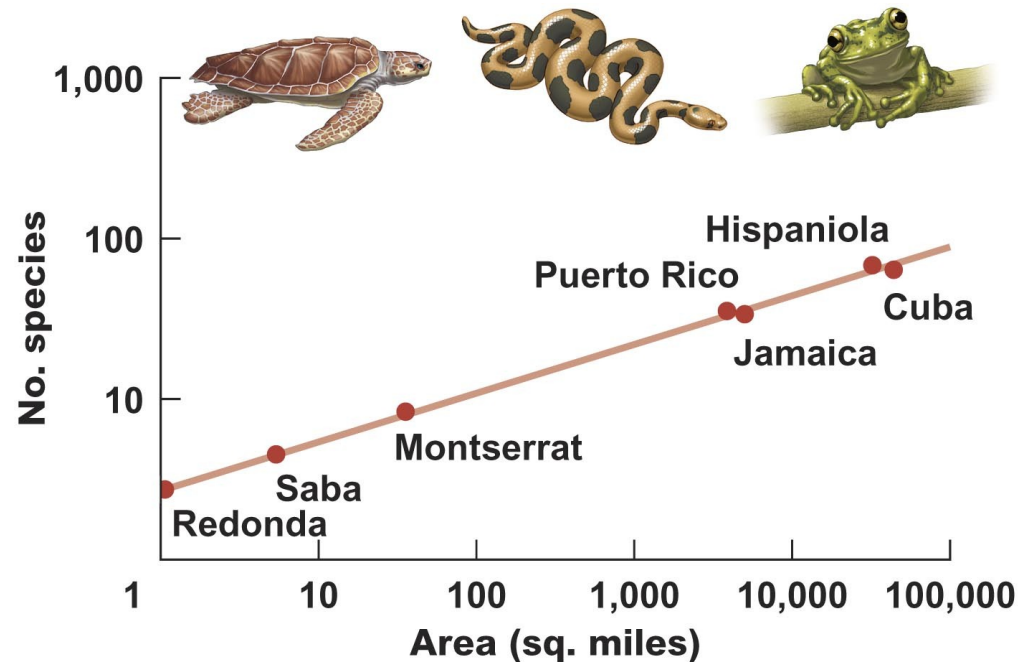
Teórica 10: Esquema conceptual

- Depredación como fuerza organizadora: redes tróficas
- Mutualismo como fuerza organizadora: redes mutualistas
- Competencia a nivel comunitario: gremios
- Importancia comunitaria: especies clave y especies dominantes
- Estabilidad comunitaria
- **Biografía de islas**

Biogeografía de islas: relación especies-área

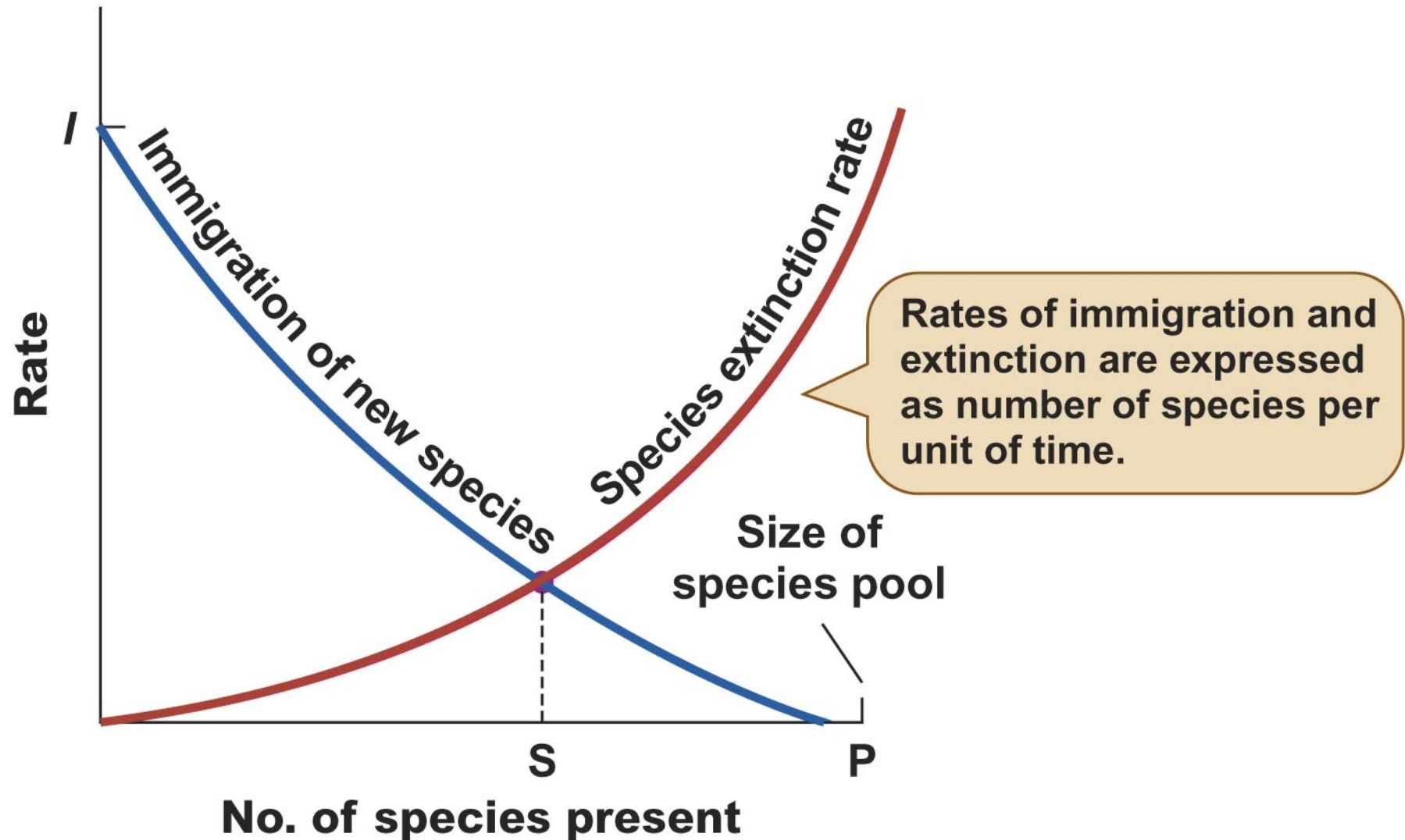


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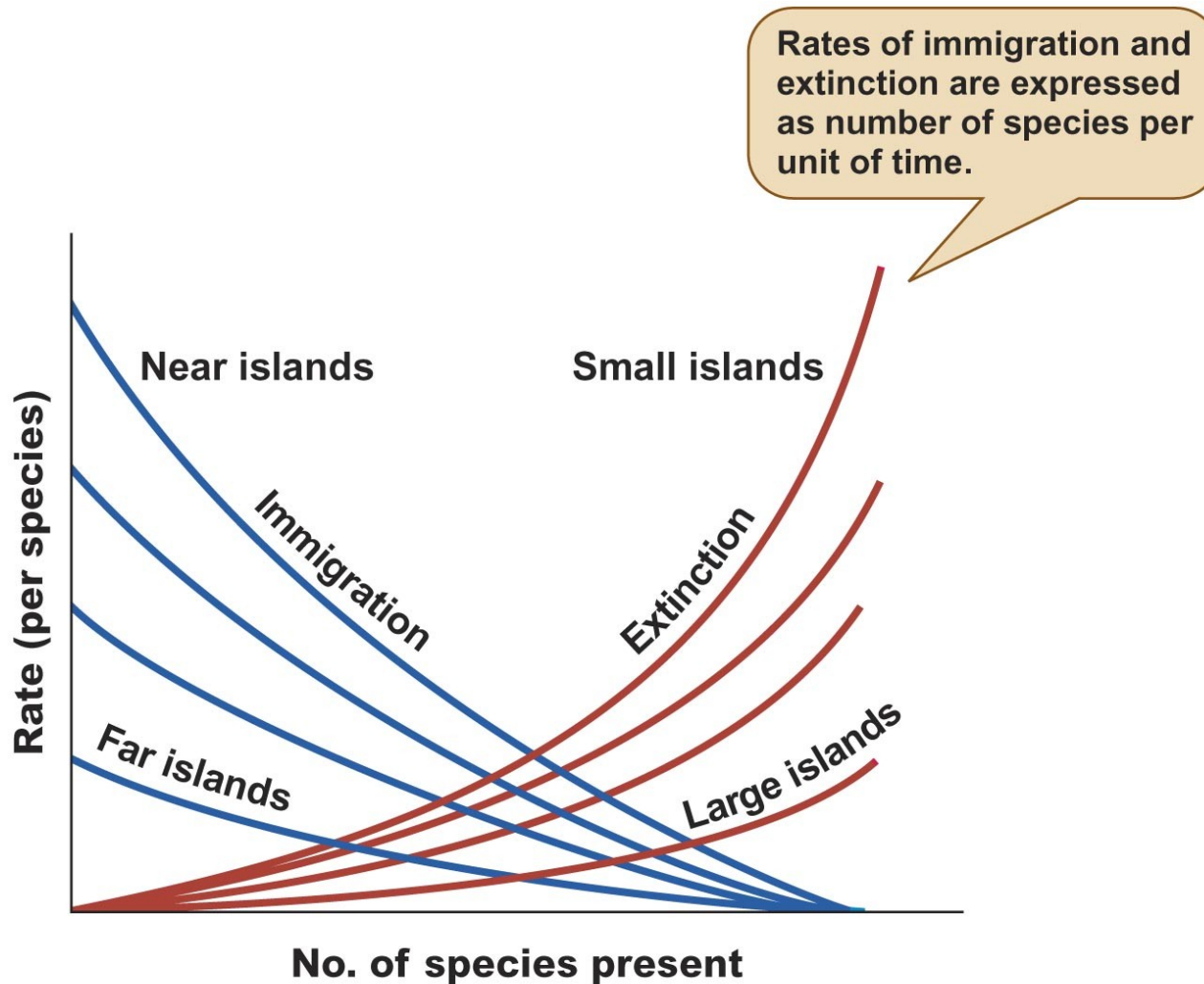


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Biogeografía de islas: Modelo de equilibrio de MacArthur y Wilson

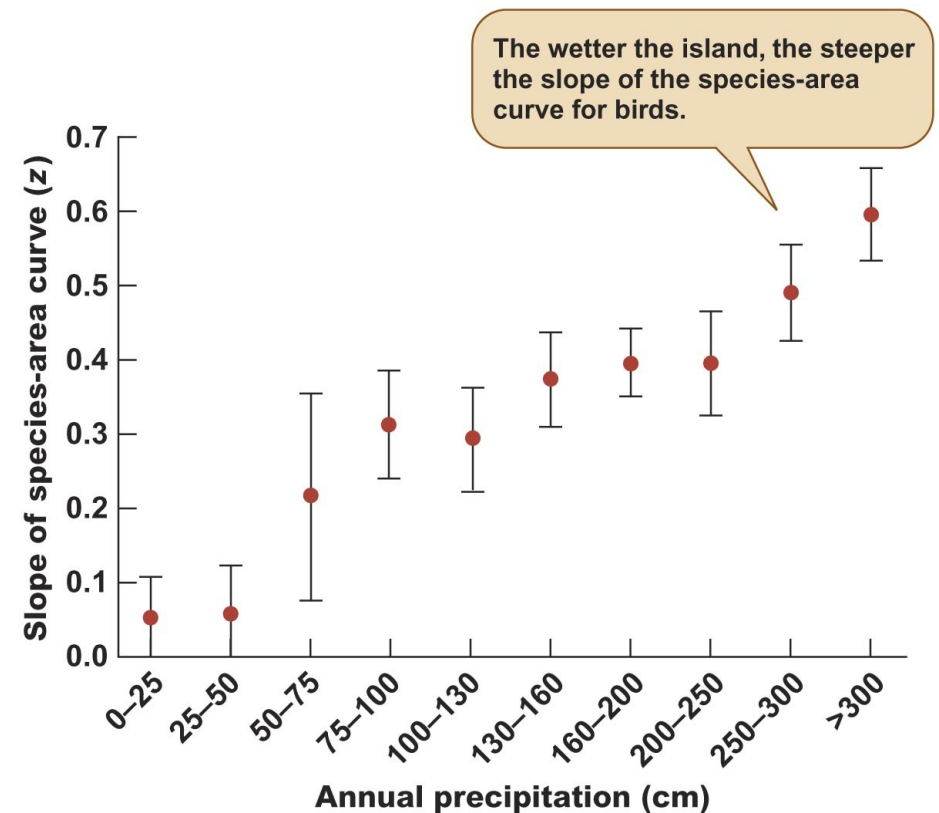
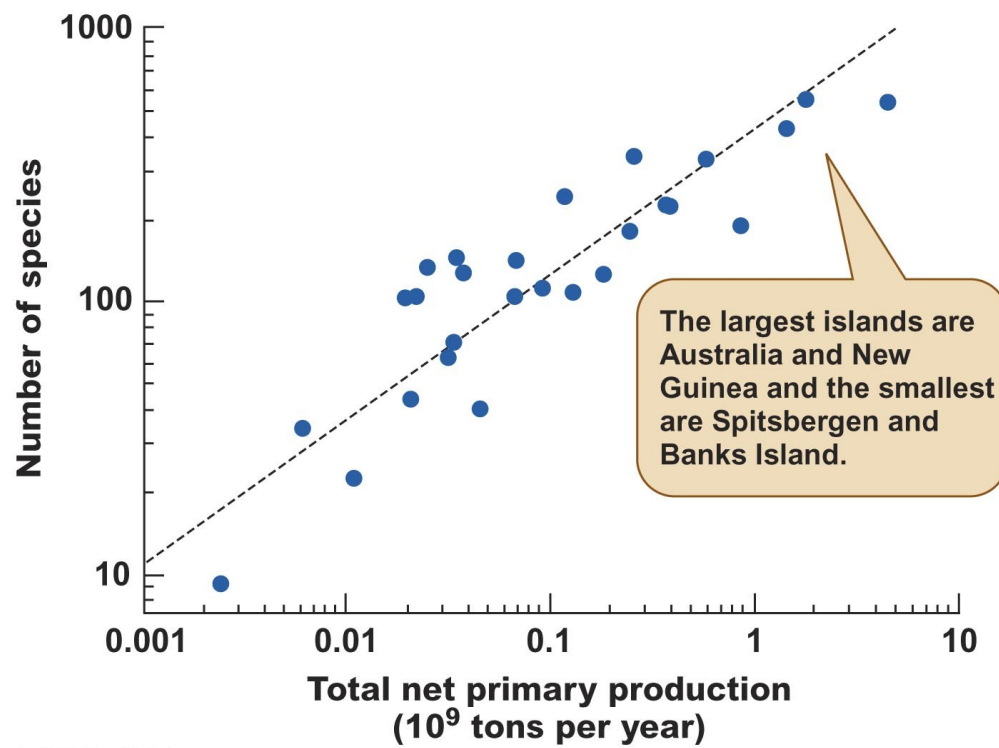


Biogeografía de islas: Modelo de equilibrio de MacArthur y Wilson



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Biogeografía de islas: Relación especies-energía



Teórica 10: Recapitulación

- Las redes tróficas permiten estudiar la influencia de la depredación como fuerza organizadora de las comunidades
- El estudio de los gremios permite evaluar la influencia de la competencia a nivel comunitario
- Las especies pueden variar en su importancia comunitaria
- La estabilidad comunitaria depende en forma compleja del número de especies y sus conexiones tróficas
- La biogeografía de islas es una teoría históricamente importante que intentó explicar la variación de la biodiversidad en archipiélagos mediante procesos de colonización y extinción