# Niches, Competition, Facilitation, and Gradients

## Paleobiology

February 08, 2016

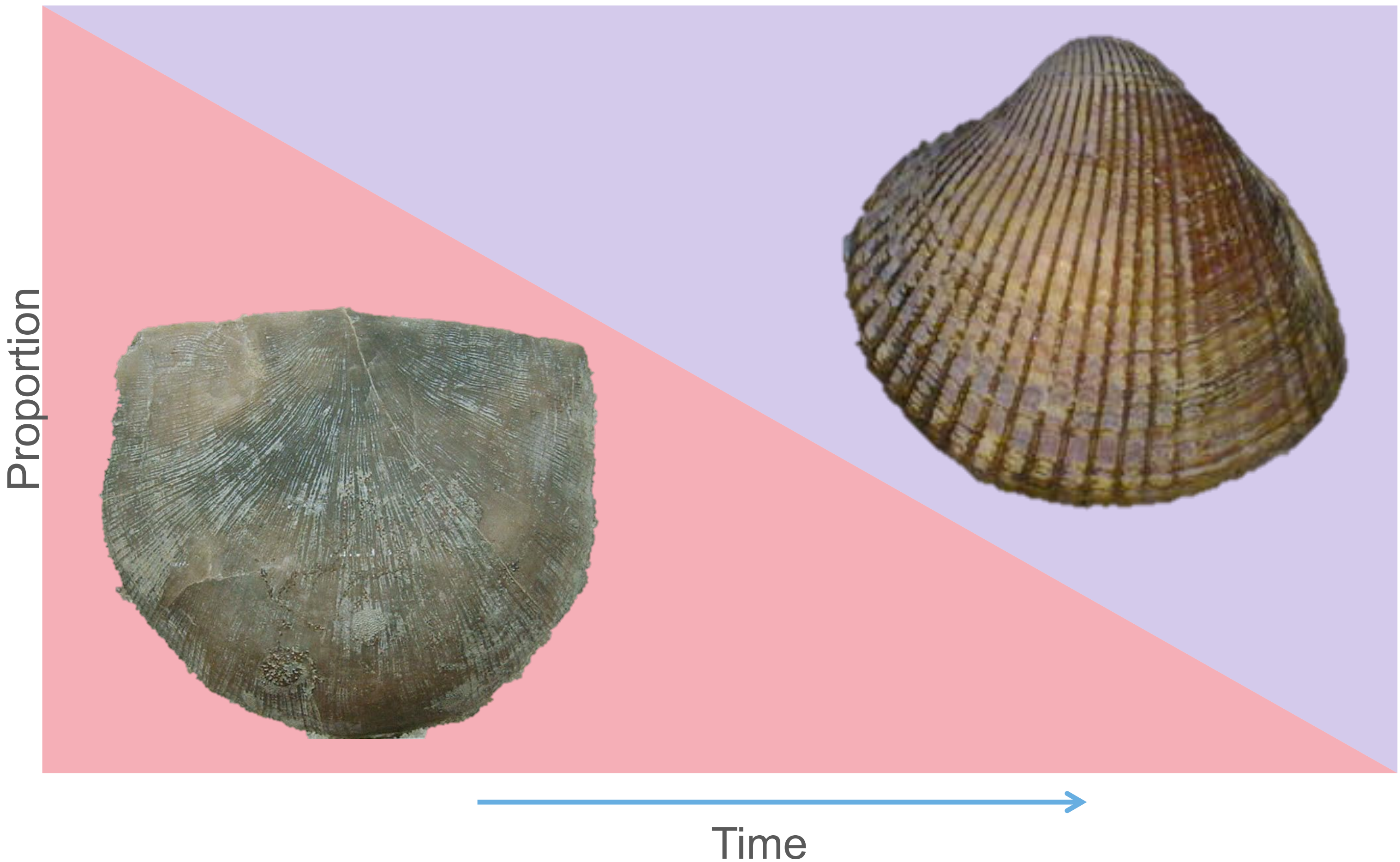
# Ecological competition

- Inter- vs. Intra- specific competiton
  - Interspecific – Between species.
  - Intraspecific – Within species.
- Interference vs. Exploitation/Resource
  - Interference – Direct fighting.
  - Exploitation – Consuming resources.


# Competitive Exclusion

- Jared Diamond’s Rules of Assembly 1975
  - (Georgii Frantsevich Gause 1932)
  - If two species are in competition, one will eventually rise to dominance and drive the other out.
    - Extirpation – Local Exclusion
    - Extinction – Global Exclusion
  - Can also be applied to clades, not just species.

# The double wedge



# Two ships passing in the night

*Paleobiology*, 6(4), 1980, pp. 383–396

## Clams and brachiopods—ships that pass in the night

Stephen Jay Gould and C. Bradford Calloway

*Abstract.*—The presumed geometry of clam and brachiopod clades (brachiopod declines matched closely by clam increases) has long served as primary data for the classic case of gradual replacement by competition in geological time. Agassiz invoked the geometric argument to assert the general superiority of clams, and it remains the standard textbook illustration today. Yet, like so many classic stories, it is not true. The supposed replacement of brachiopods by clams is not gradual and sequential. It is a product of one event: the Permian extinction (which affected brachiopods profoundly and clams relatively little). When Paleozoic and post-Paleozoic times are plotted separately, numbers of clam and brachiopod genera are positively correlated in each phase. Each group pursues its characteristic and different history in each phase—clams increasing, brachiopods holding their own. The Permian extinction simply reset the initial diversities. The two groups seem to track each other in each phase and a plot of brachiopod vs. clam residuals (each from their own within-phase regressions against time) yields significantly positive association. Some of this tracking may be an artifact of available rock volumes; we could, however, detect no effect of stage lengths. Passive extrapolation of microevolutionary theory into the vastness of geological time has often led paleontologists astray. Competitive interaction may rule in local populations, but differential response to mass extinctions (surely not a matter of conventional competition) may set the relative histories of large groups through geological time. Similarly, adaptive superiority in design cannot, in the usual sense of optimal engineering, have much to do with the macroevolutionary success of clams. The interesting question lies one step further back: what in the inherited *Bauplan* of a clam permits flexibility in design and why are other groups, however successful in their own domain, unable to alter their basic design.

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# Two ships passing in the night

ECOLOGY LETTERS

*Ecology Letters*, (2015) **18**: 1030–1039 doi: 10.1111/ele.12485

LETTER

## Ecological interactions on macroevolutionary time scales: clams and brachiopods are more than ships that pass in the night

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**Abstract**

Competition among organisms has ecological and evolutionary consequences. However, whether the consequences of competition are manifested and measureable on macroevolutionary time scales is equivocal. Marine bivalves and brachiopods have overlapping niches such that competition for food and space may occur. Moreover, there is a long-standing debate over whether bivalves outcompeted brachiopods evolutionarily, because brachiopod diversity declined through time while bivalve diversity increased. To answer this question, we estimate the origination and extinction dynamics of fossil marine bivalve and brachiopod genera from the Ordovician through to the Recent while simultaneously accounting for incomplete sampling. Then, using stochastic differential equations, we assess statistical relationships among diversification and sampling dynamics of brachiopods and bivalves and five paleoenvironmental proxies. None of these potential environmental drivers had any detectable influence on brachiopod or bivalve diversification. In contrast, elevated bivalve extinction rates causally increased brachiopod origination rates, suggesting that bivalves have suppressed brachiopod evolution.

**Keywords**

Capture-recapture, fossil, geochemical proxy, Ornstein-Uhlenbeck model, Phanerozoic, Red Queen, sea level, stochastic differential equations (SDEs), time series.

*Ecology Letters* (2015) **18**: 1030–1039

# Ecological facilitation

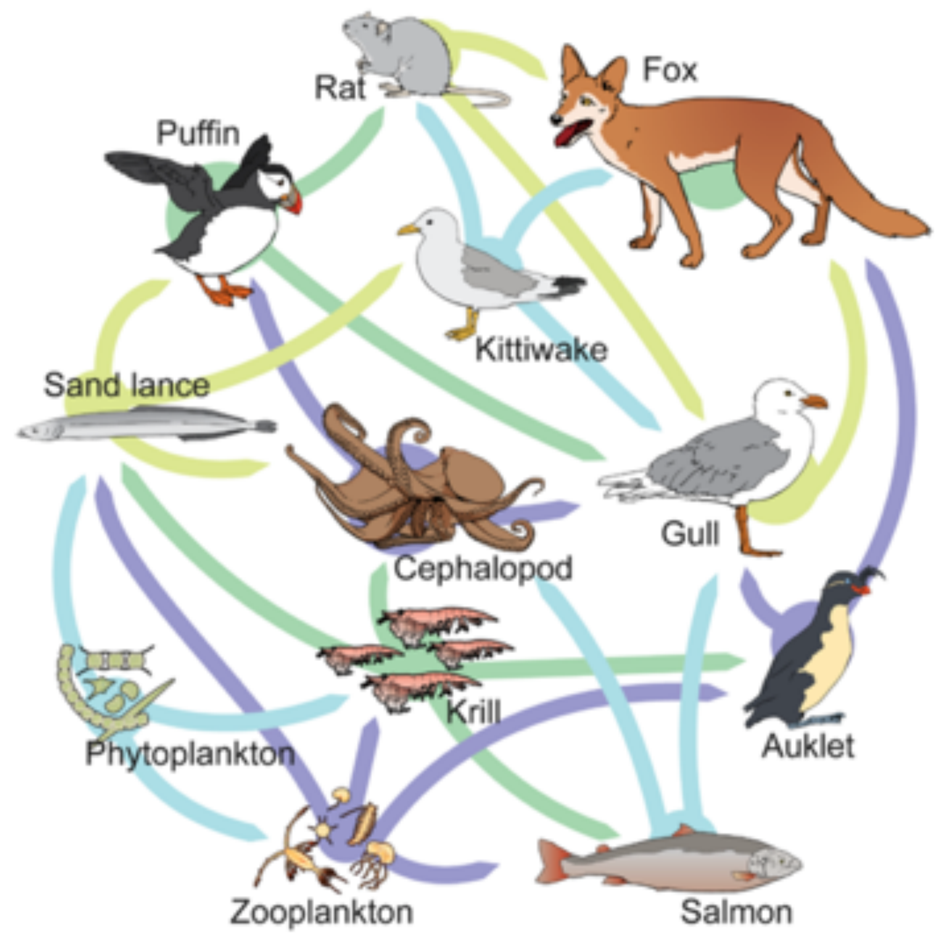
- Mutualism – Interactions are beneficial to both.
- Commensalism – Interactions benefit one, and are neutral towards the other.
  - Phoresy – One animal using another for transport (no eating!).
  - Inquilinism – Using another organisms' home.
  - Metabiosis – Another organism indirectly alters the environment, paving the way for another.

# The Eltonian Niche

- Charles Elton (1927)
  - What is the “function” of a species in its ecosystem?
  - Using ecosystem in the definition implies a certain underlying philosophical belief about ecological behaviors.
  - This is most commonly expressed in terms of *trophic level.*

# Trophic level

- The position of an organism is a food chain or web.

# Inferring trophic relationships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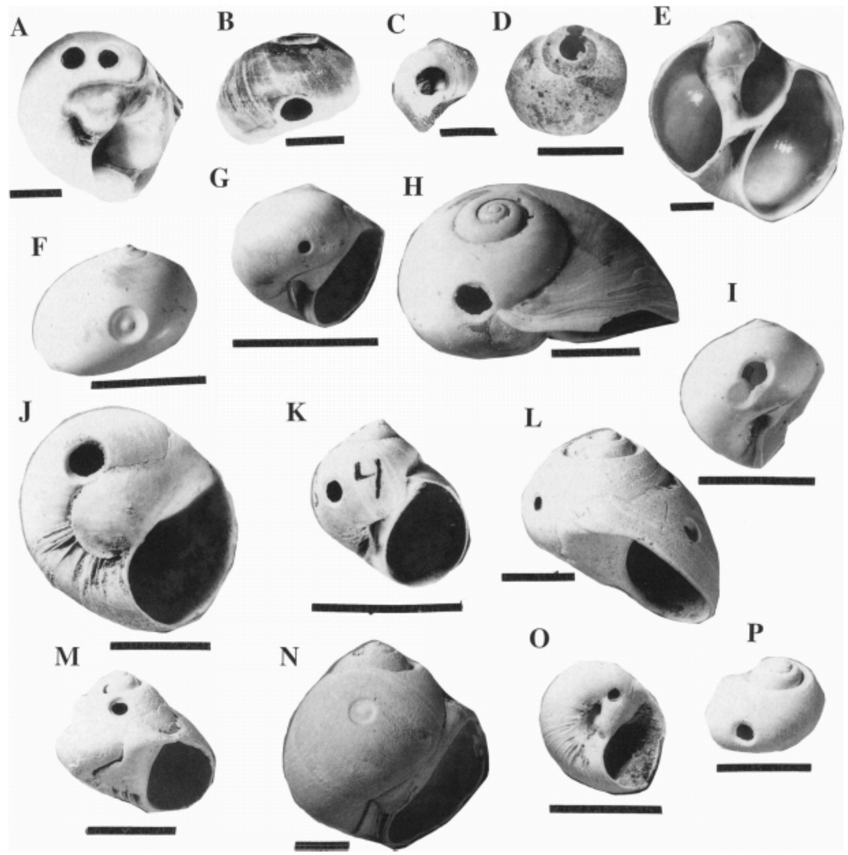

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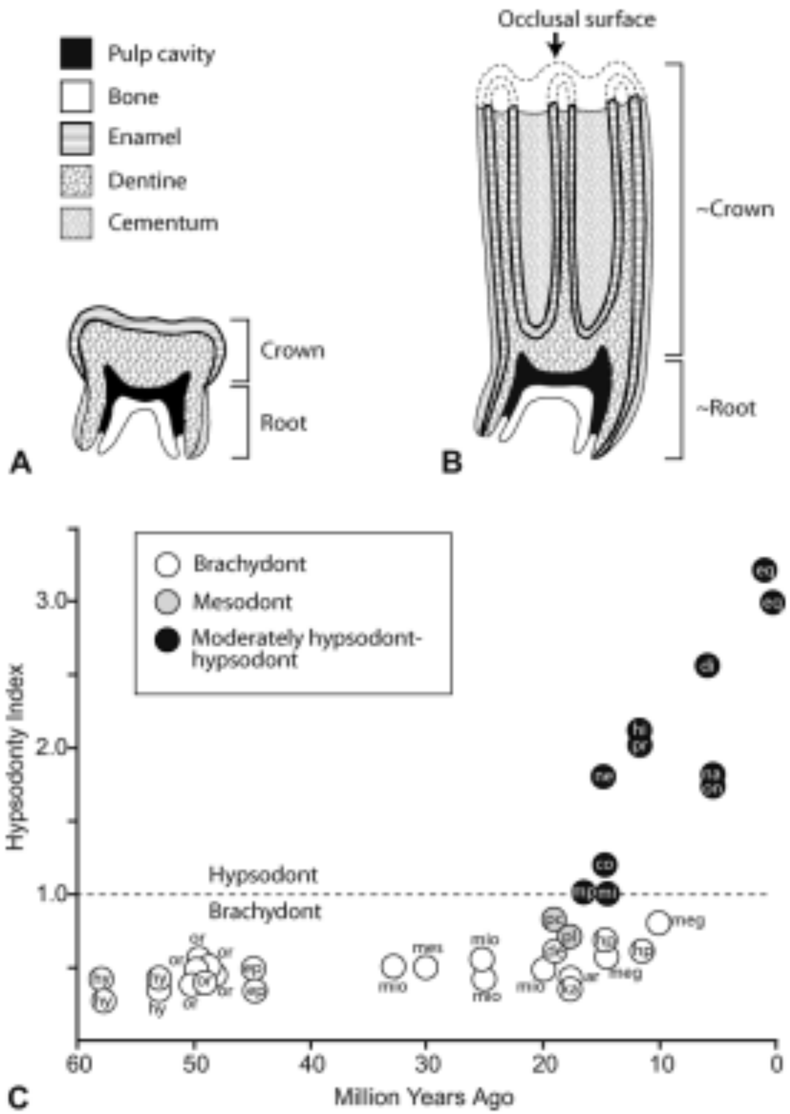
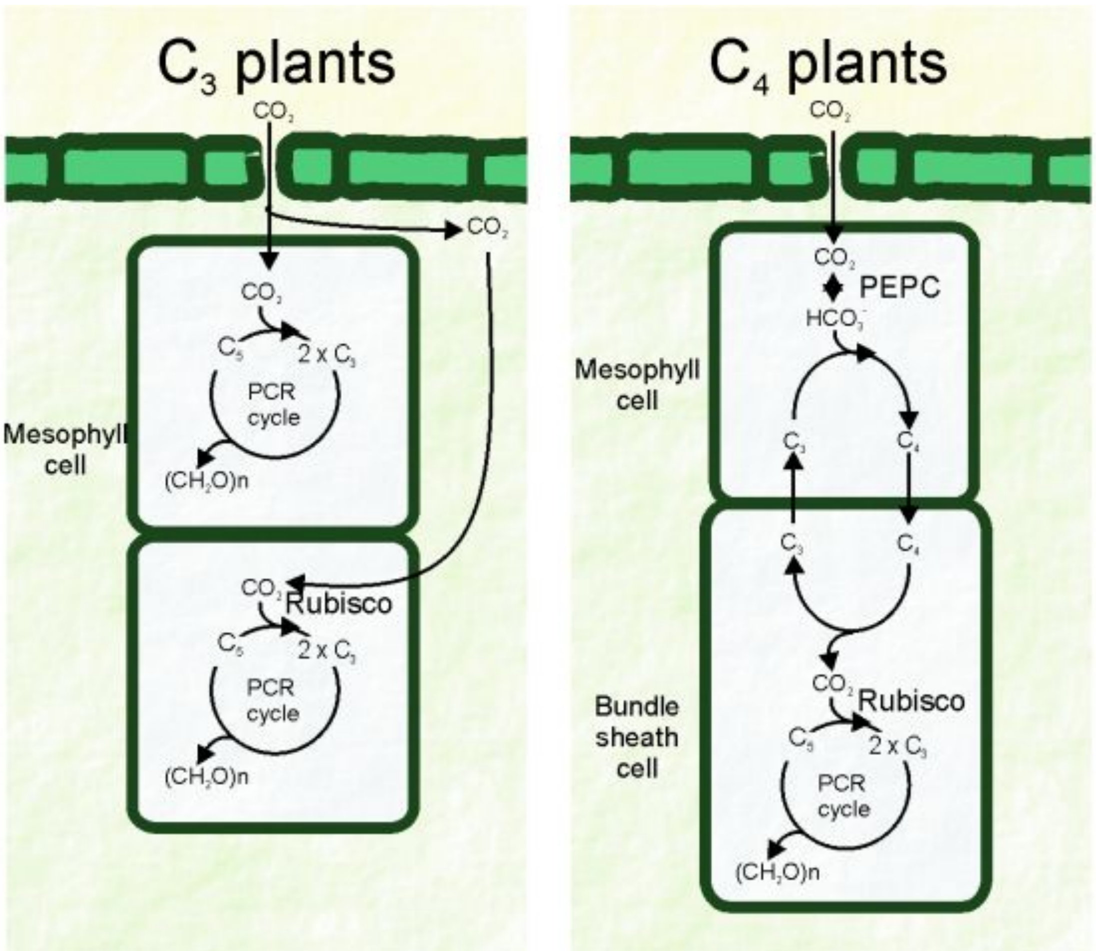
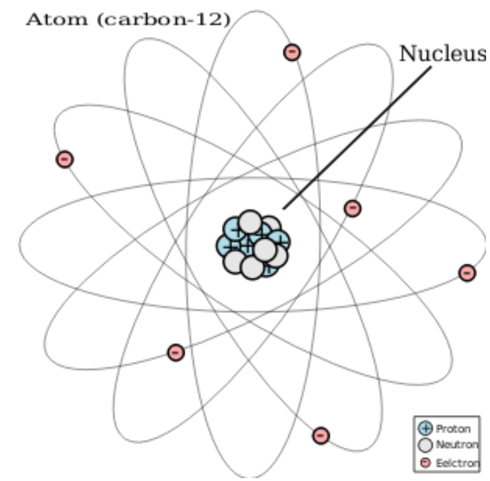



- Brachyodonts are primarily associated with browsing.
- Browsing – Eat leaves, bark, and green stems from plants
- Examples – Deer, Giraffe
- Hypsodonts are primarily associated with grazing.
- Grazers clip vegetation at or near ground level - i.e., eat grasses.
- Examples – Sheep, Cows

# Inferring the trophic relationships




Isotope

$$\sim\delta^{13}C = \frac{\text{Sample: } ^{13}C/^{12}C}{\text{Standard: } ^{13}C/^{12}C}$$

# The Eltonian Niche

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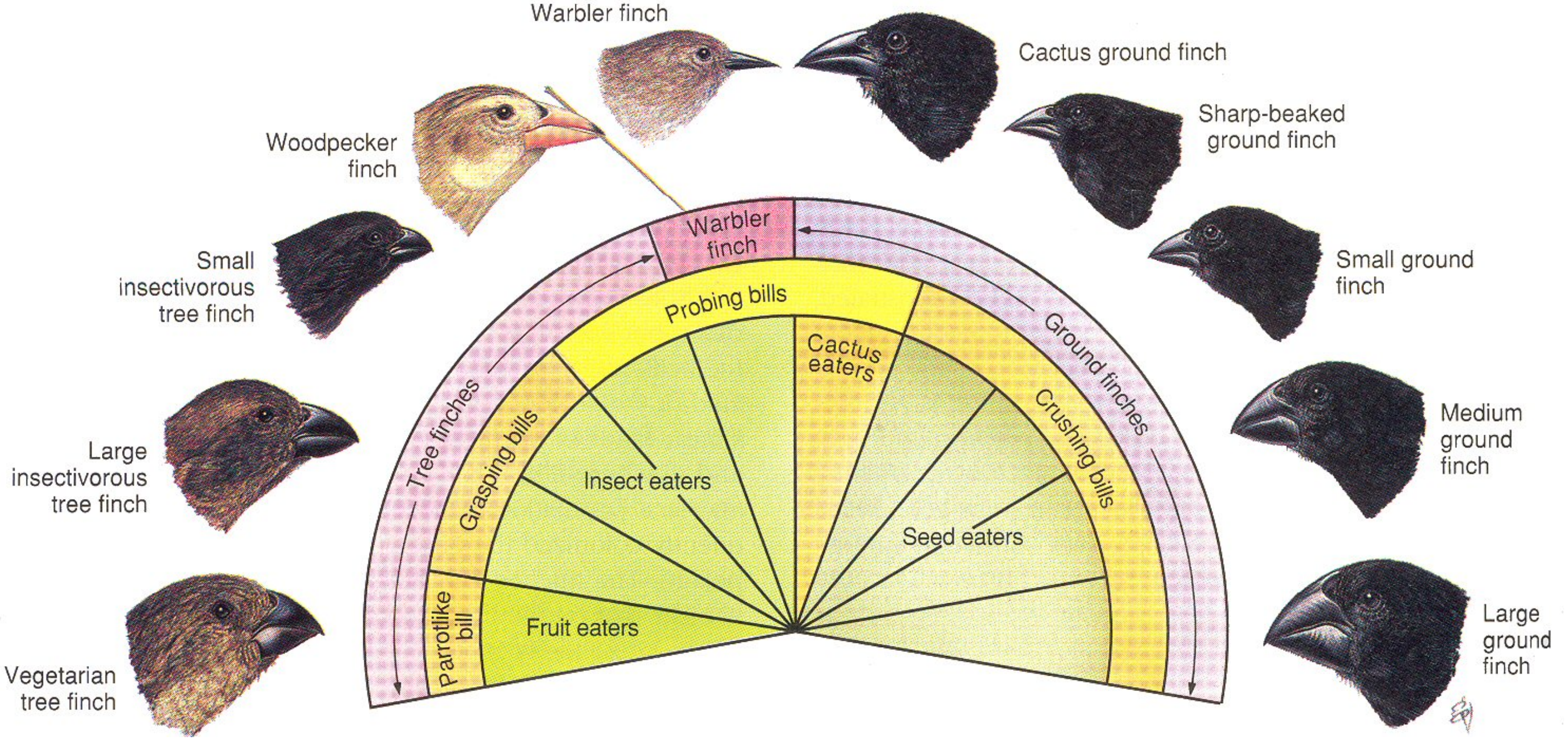
  - Using ecosystem in the definition implies a certain underlying philosophical belief about ecological behaviors.
  - This is most commonly expressed in terms of *trophic level*
    - Can also be expressed in terms of *what* is being eaten, as opposed to a level.
    - Taxa can have functions other than eating things. These functions are rarely used to define niches… metabiosis



# Resource Partitioning

- Implicit in the Eltonian niche concept is the idea of resource or niche partitioning.



# Alternative terminology

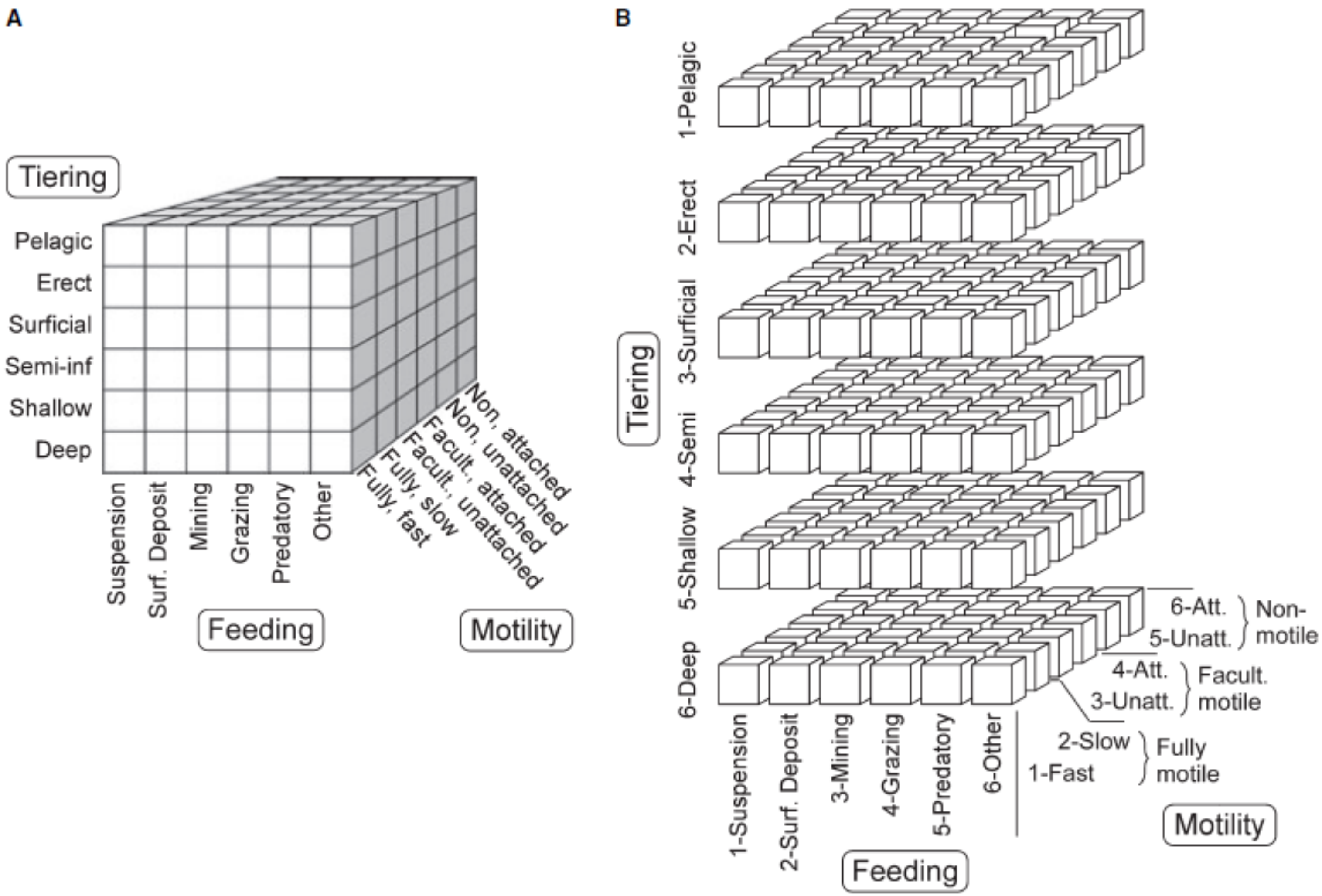
- Use Trophic Level or Trophic Position – To describe a group of taxa that use the same food resource.
- Use Guild or Megaguild – To describe a group of taxa that utilize the same suite of resources (not just food).
- Use Habit or Mode – To describe how (behaviorally or physiologically) a taxon utilizes a resource.
- Use Resource Partitioning – To describe the development of different habits to utilize the same resource.
- ***Avoid the use of the word niche entirely in these contexts.***

# Alternative terminology

- Trophic Level - Herbivore
- Habit - Grazer
- Guild – Sheep, Horses, Cows; Animals found in approximately the same habitat that are also herbivorous grazers.
- Megaguild – Sheep, Horses, Cows, Kangaroos, Hippos; All animals that are also herbivorous grazers.

What about me?

# Ecospace



A
Tiering
Pelagic
Erect
Surficial
Semi-inf
Shallow
Deep
Suspension
Surf. Deposit
Mining
Grazing
Predatory
Other
Fully, fast
Fully, slow
Facult., unattached
Facult., attached
Non, unattached
Non, attached
Feeding
Motility
B
Tiering
1-Pelagic
2-Erect
3-Surficial
4-Semi
5-Shallow
6-Deep
1-Suspension
2-Surf. Deposit
3-Mining
4-Grazing
5-Predatory
6-Other
Feeding
6-Att.
5-Unatt.
Non-motile
4-Att.
3-Unatt.
Facult. motile
2-Slow
1-Fast
Fully motile
Motility

# The Grinellian niche

- Joseph Grinell (1917)
  - The set of conditions that permit a species to exist in a particular location.
    - The set of conditions is not the same as the location.
    - What is the meaning of existence?
    - Are these “conditions” physical or biological?
    - If biological, do we mean intra-specific or inter-specific.
    - Do we mean behavioral or physiological, or both?

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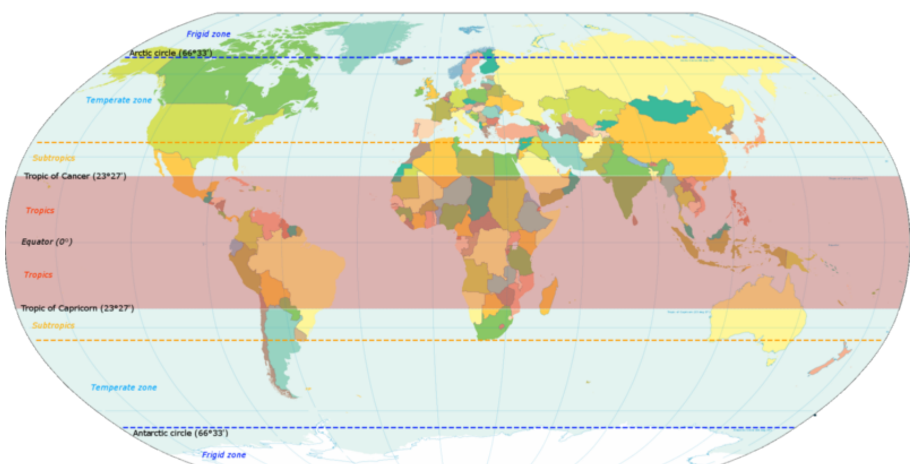
Latitude




Warm and Wet

# Gradient ecology

- Robert Whittaker 1967
  - Shelford's Law of Tolerance

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- Robert Whittaker 1967
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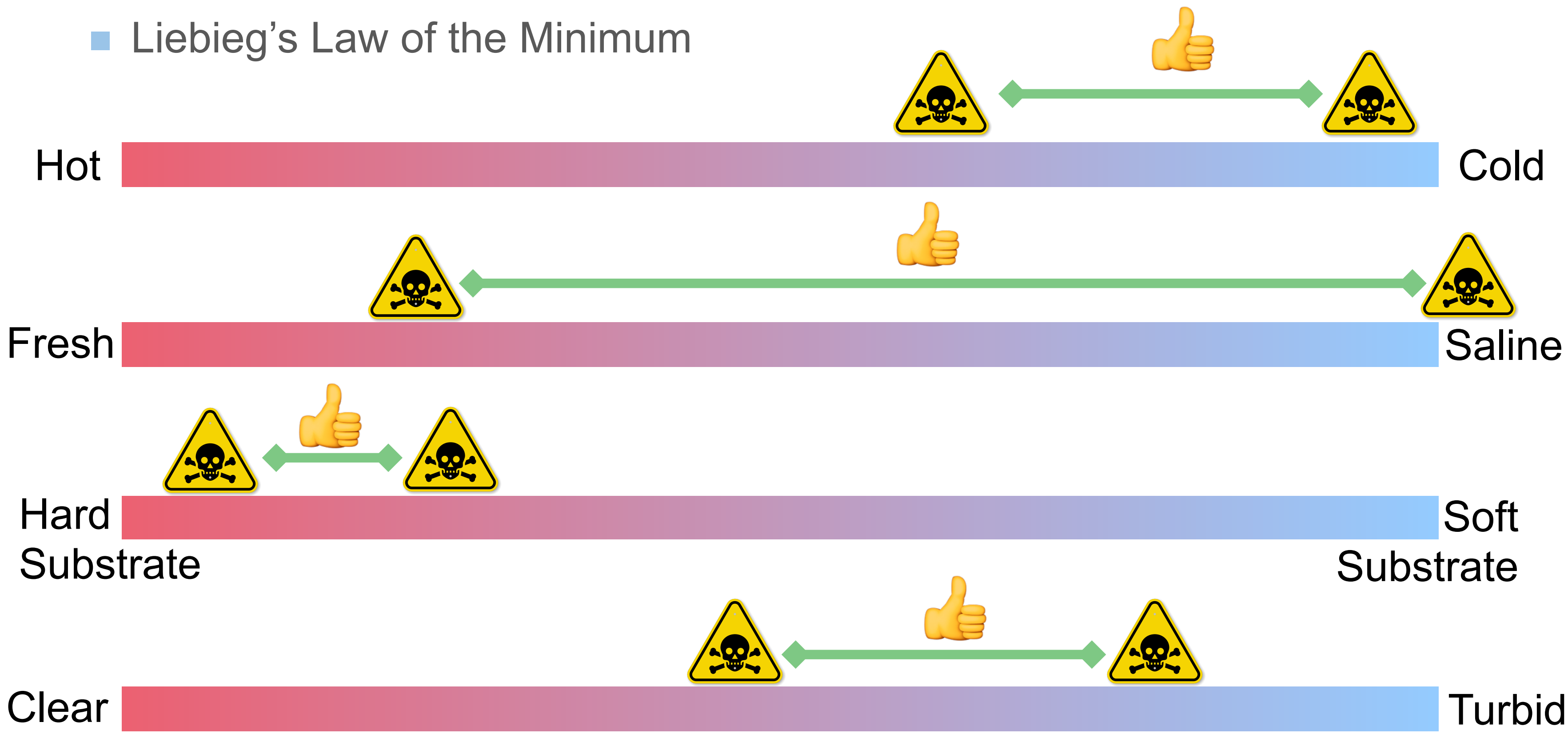
  - Liebieg's Law of the Minimum



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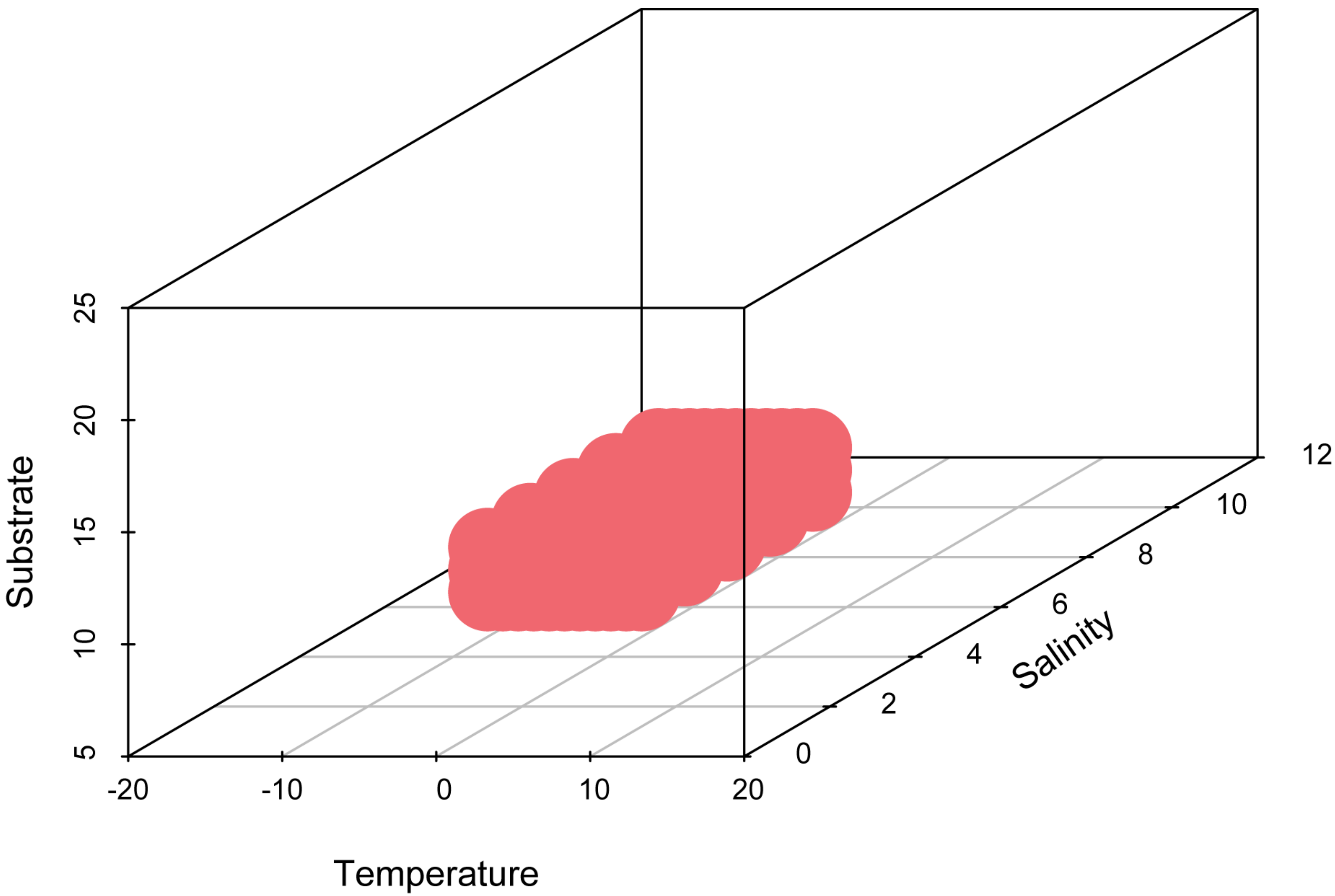
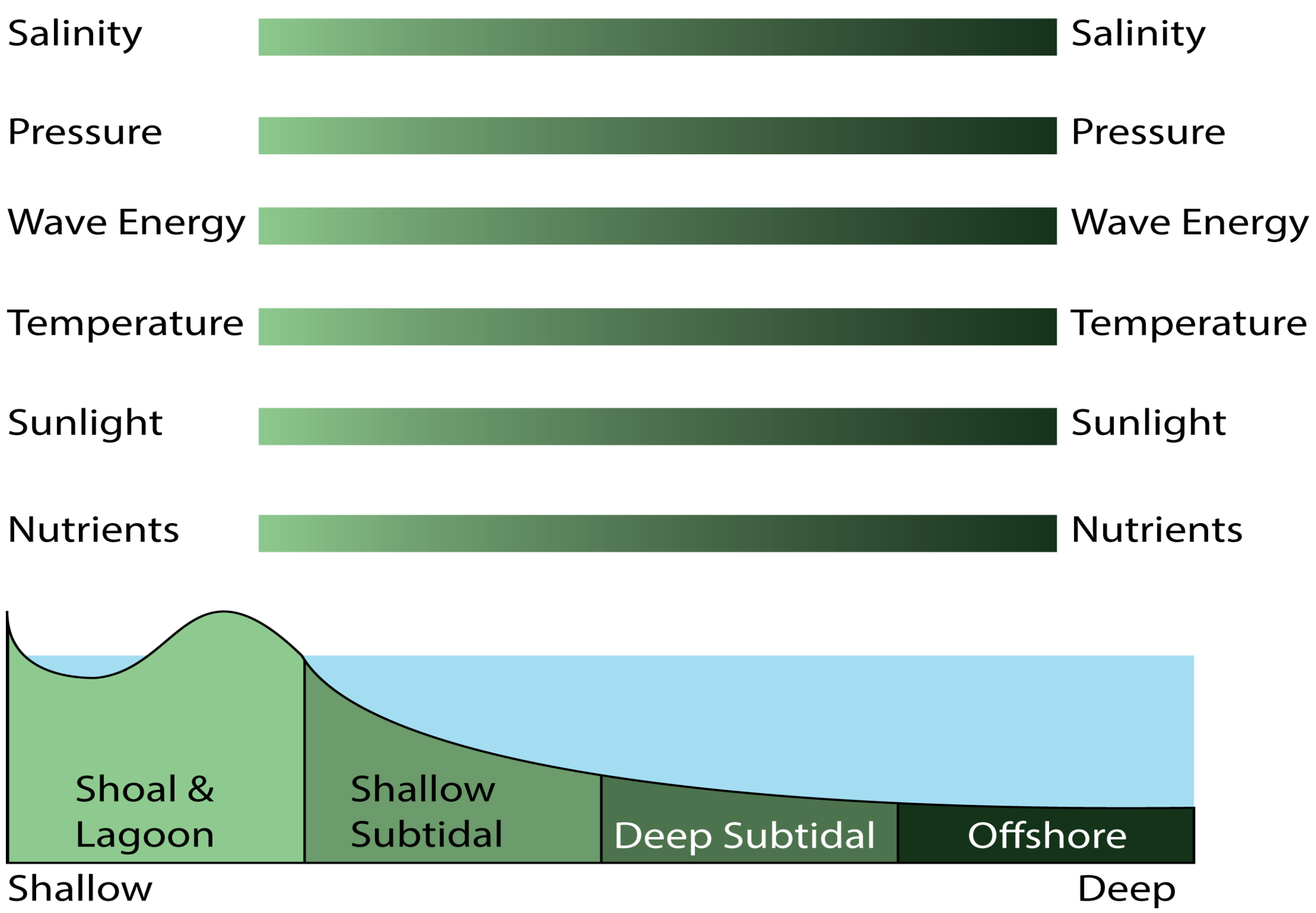


# Inferring the Grinellian niche

- Complex (Indirect) gradients



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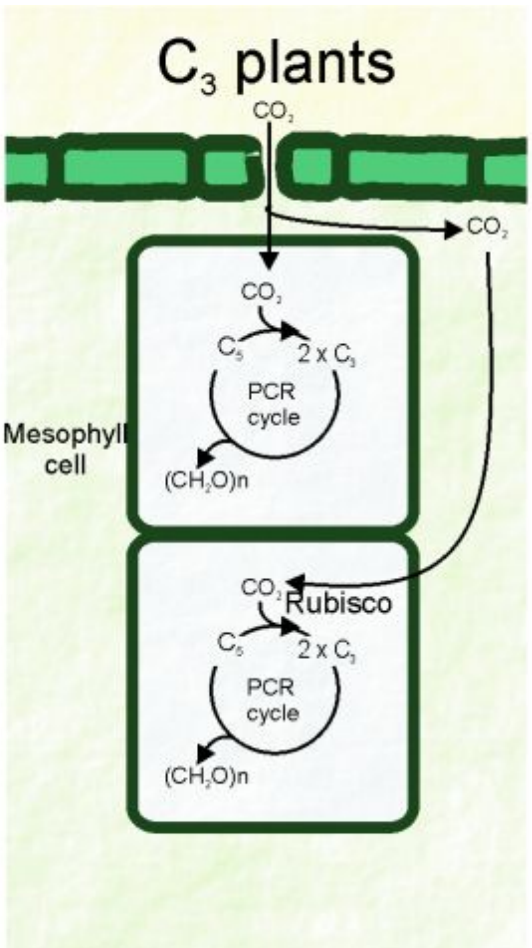


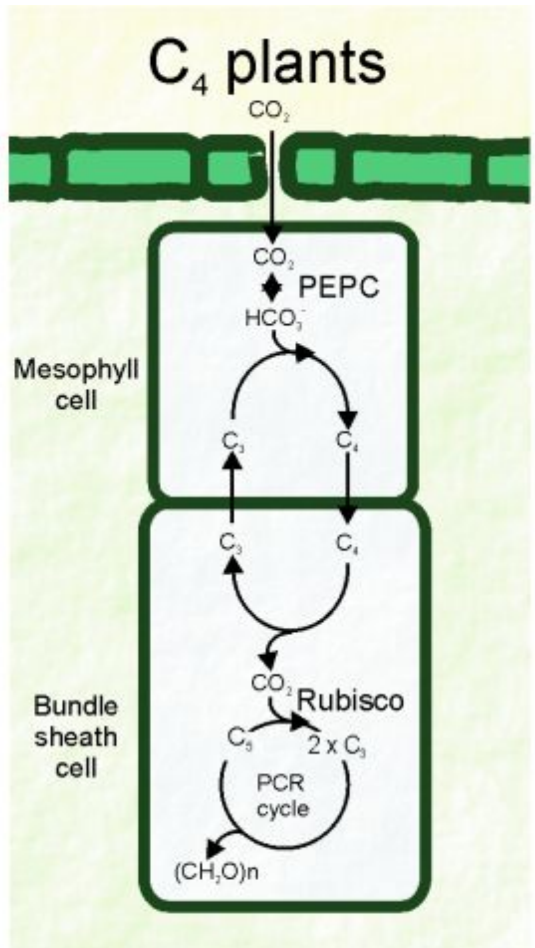


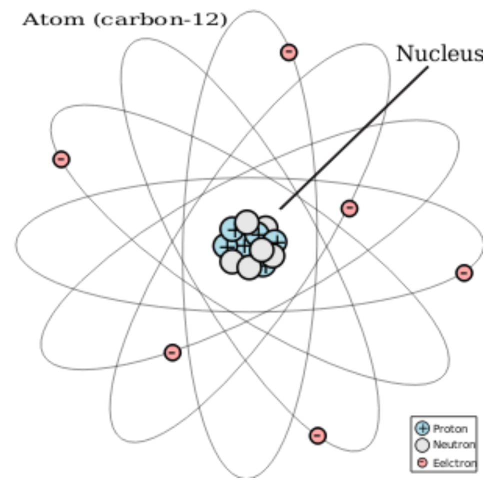


Isotope

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# The Hutchinsonian niche

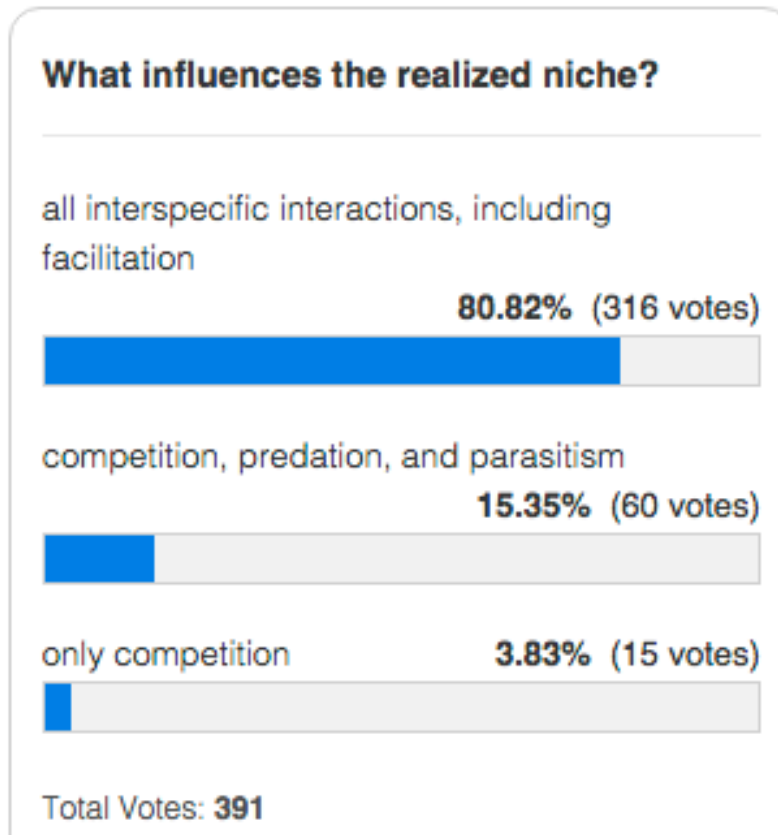
- George Evelyn Hutchinson (1957)
  - An expansion and clarification of the Grinellian Niche.
  - To boldly take a risk-free stance.
- Splits the Grinellian niche into three components
  - The fundamental niche – The niche a species could hypothetically occupy based on its physiological tolerances.
  - The realized niche – The niche a species is observed to occupy
  - The potential niche – Is the difference between the fundamental and realized niche.
    - Note: The fundamental niche, by definition, must always be greater than or equal to the realized niche.

# Why is the realized niche smaller?

- Maybe the species is young and has not yet had time to spread to all possible environments it could physiologically tolerate.
- Maybe there are geophysical barriers (i.e., mountain chain, oceans) preventing species from dispersing into new areas of its fundamental niche
- Maybe interspecific competition is strong, which limits the population size and dispersal ability of the taxon, preventing it from moving into new areas of its fundamental niche.
- Maybe intraspecific competition is strong, which limits the population size and dispersal ability of the taxon, preventing it from moving into new areas of its fundamental niche.
- Maybe the portions of its fundamental niche are not currently expressed in the real world.

# A hypothesis is not a definition

- Hutchinson hypothesized that interspecific competition controls the realized niche.
- This has led to a series of unfortunate misconceptions about the realized niche.
  - Inter-specific competition only.
  - Biological vs. Abiological.
- The benefit of the fundamental vs. realized paradigm is that we can easily formulate hypotheses about why the difference exists.



# Why this matters…

Opinion TRENDS in Ecology and Evolution Vol.18 No.3 March 2003 119

ELSEVIER

## Inclusion of facilitation into ecological theory

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**Investigations of the role of competition, predation and abiotic stress in shaping natural communities were a staple for previous generations of ecologists and are still popular themes. However, more recent experimental research has uncovered the largely unanticipated, yet striking influence of facilitation (i.e. positive species interactions) on the organization of terrestrial and aquatic communities. Modern ecological concepts and theories were well established a decade before the current renaissance of interest in facilitation began, and thus do not consider the importance of a wide variety of facilitative interactions. It is time to bring ecological theory up to date by including facilitation. This process will not be painless because it will fundamentally change many basic predictions and will challenge some of our most cherished paradigms. But, ultimately, revising ecological theory will lead to a more accurate and inclusive understanding of natural communities.**

during the development of modern ecological theory [1,2]. As a result, current theory considers only the negative interactions and abiotic factors that deplete populations and remove species, and largely ignores the credit column of the ecological ledger. Our purpose here is to begin to amend this oversight. We consider how inclusion of facilitation into the theory, models and paradigms of population and community ecology can alter many basic predictions, and argue that this is crucial to our understanding and conservation of natural communities.

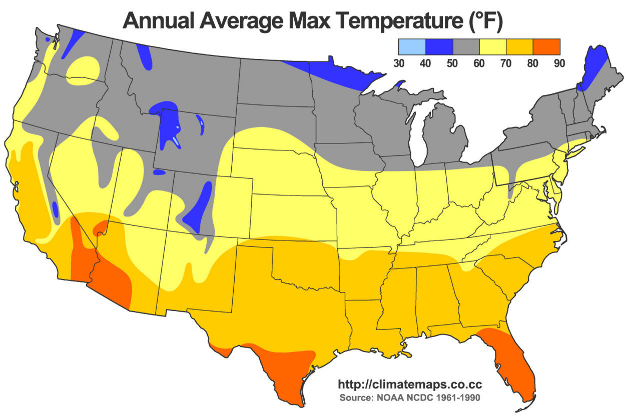
### Facilitation and the niche

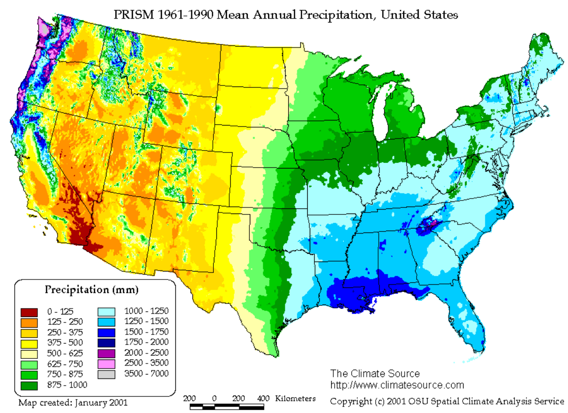
Including facilitation in the niche concept can alter the relationship between the fundamental and realized niche as well as predictions of where a species can and will live in the physical world. Because the niche is a core principle, these changes cascade through the theoretical landscape of ecology. Originally defined by Grinell [7] and Elton [8], the idea was refined in 1957 by Hutchinson [9] when he

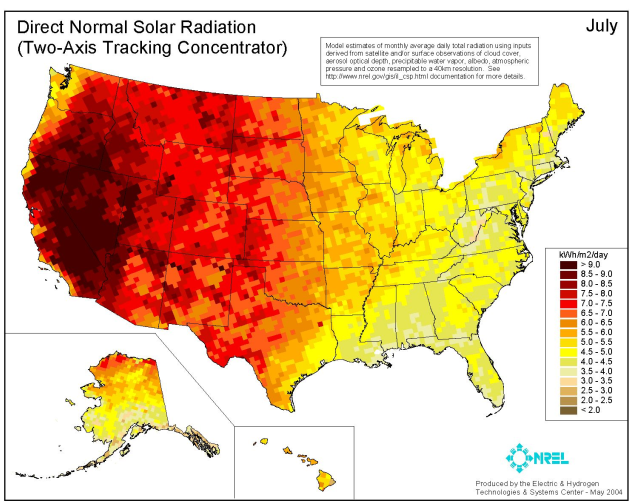
- Species A cannot physically tolerate living in a particular area.
- Species B comes along and alters the surrounding conditions.
- The species can now live in this area thanks to this act of ecological facilitation.
- Does this mean the realized niche is now larger than the fundamental niche?

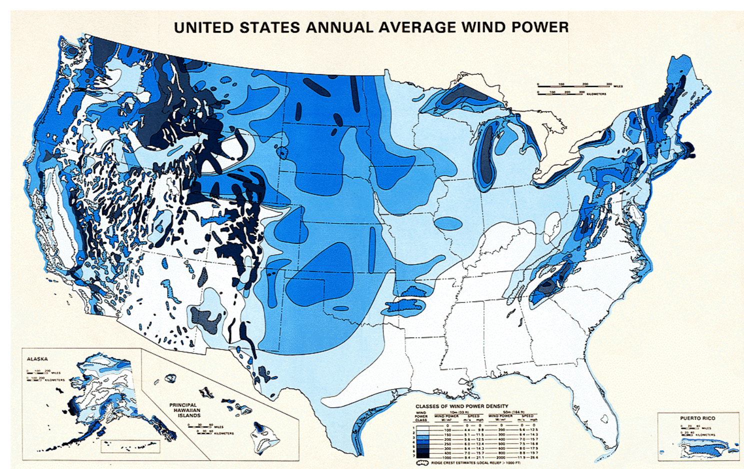
# Niches and geographic range

- Environmental dimensions that make up niches all have a spatiotemporal distribution.



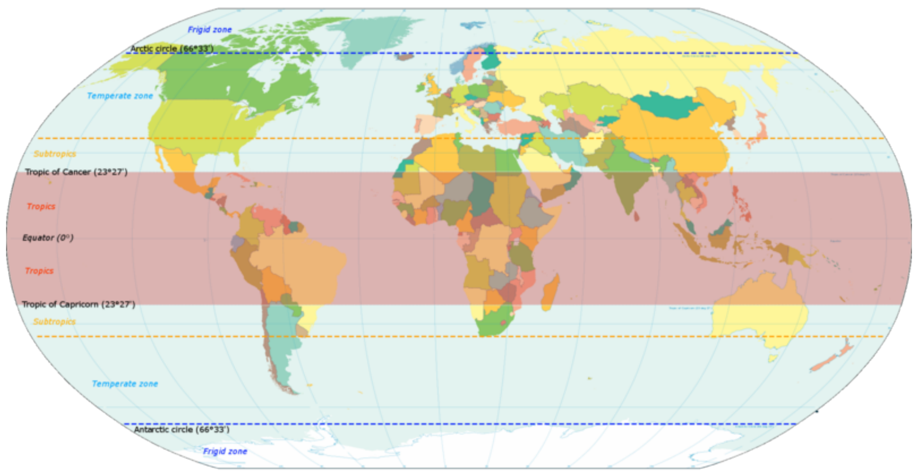



# The “habitat” problem

- A habitat is an ecological or environmental area that is inhabited by a particular species of animal, plant, or other type of organism. A place where a living thing lives is its habitat.

Latitude




Warm and Wet

# A habitat is the niche of a location

- ~~A habitat is an ecological or environmental area that is inhabited by a particular species of animal, plant, or other type of organism. A place where a living thing lives is its habitat.~~

- Think of habitat as the niche of a hypothetical taxon – e.g., the tropical taxon, the deep-sea taxon.
  - A suite of environmental variables that can be found at one or more locations.

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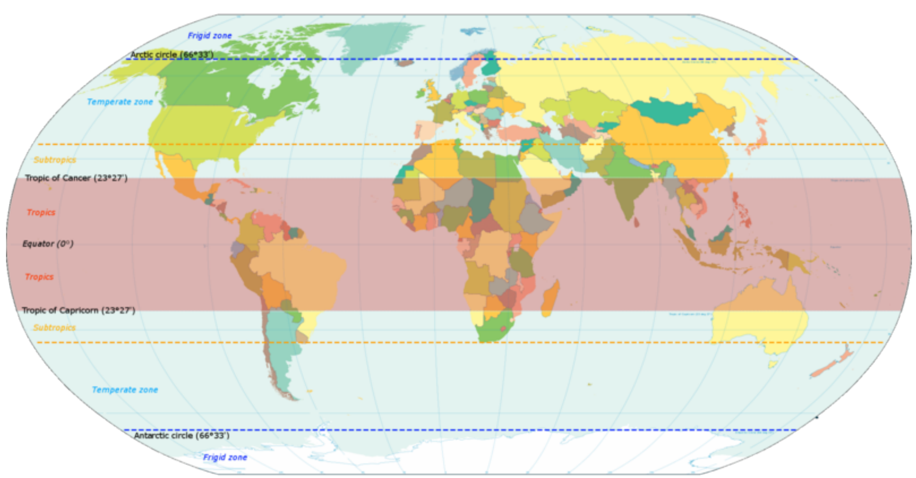


Warm and Wet

# Bioclimatic envelopes

- Measure the fundamental "climatic" niche of a species.
- Generate a mathematical model that predicts future climate.
- Assume that the species will occupy all areas where that climate will be.