Maintenance of Diversity – Exploring models and hypotheses with trees

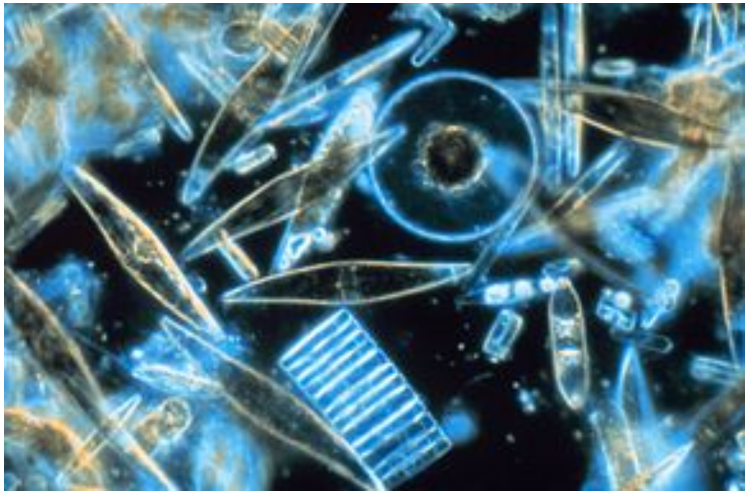
Understand niche partitioning and storage effects on diversity

Explore frequency-dependent hypotheses: niche complementarity, negative density dependence, Janzen-Connell hypothesis

Consider the unified neutral theory of biodiversity and biogeography

Paradox of the Plankton

From the "Paradox of the Plankton" G. Evelyn Hutchinson asked the question of how so many species of plankton could cohabit the same waters?



All have similar requirements in what they need:
light, carbon dioxide, nutrients

Shouldn't they compete interspecifically?

Why shouldn't a few or one species prevail over time?

Paradox of the Trees

We can apply the same question to a tropical rain forest

How do ~300 species in a hectare (100m x 100m) coexist?

The 'needs of trees' are pretty basic: light, moisture, carbon dioxide, minerals. … What else?

"Diversity of trees in Ecuador's Amazon rainforest defies simple explanation" – Smithsonian Tropical Research Institute

1100 tree species can be found in a a 25-hectare area

How do so many species indefinitely coexist??

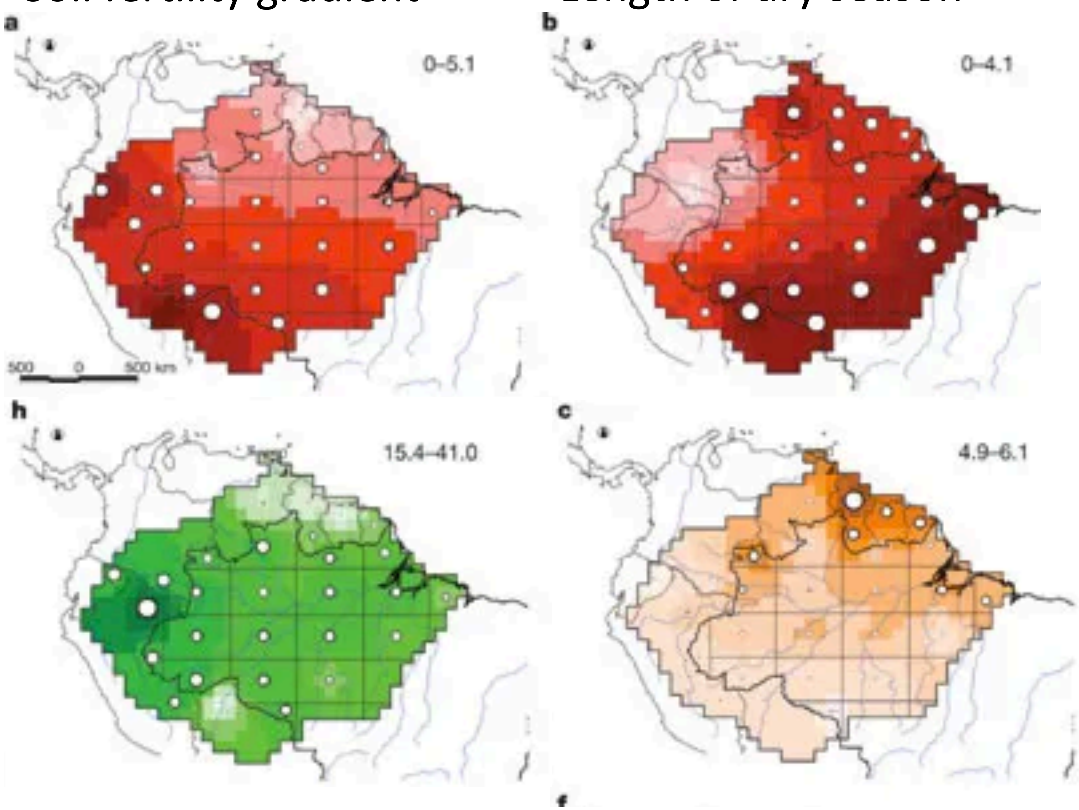
Forest Dynamics Plots (FDP) Network

Floristic patterns across Amazonia

Major factors influencing gamma (regional) diversity?

Inventories of tree diversity across the Amazon basin and Guiana shield (89 families and 513 genera) showed two dominant gradients:

Soil fertility gradient   Length of dry season



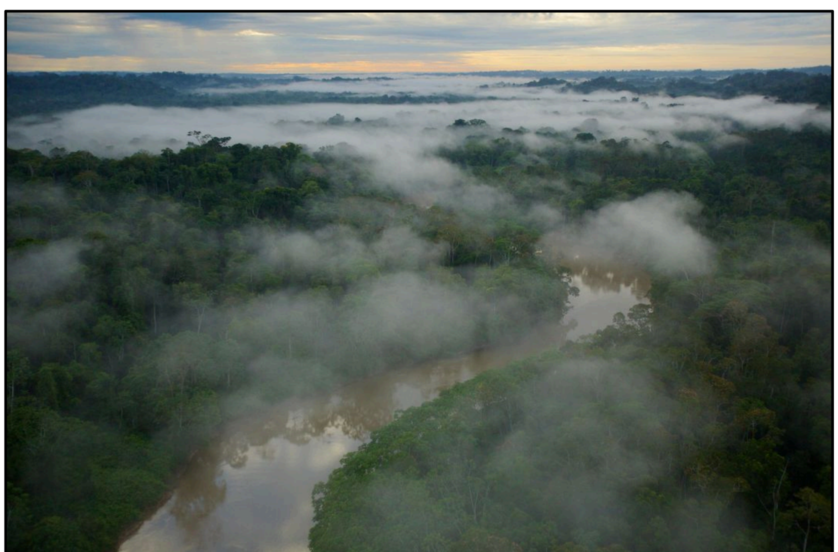
Overall patterns of diversity show highest diversity in western Amazon basin

Tree genera on the Guiana shield grew on poor soils (older soils ~ fewer nutrients) Showed denser wood, larger seeds

ter Steege et al. 2006, *Nature*

Paradox of the Trees

Yasuni National Park - Ecuador



Yasuní Forest Dynamics Plot (FDP)

- 25-ha plot containing over 150,000 mapped trees ≥1 cm at DBH for over 1100 species

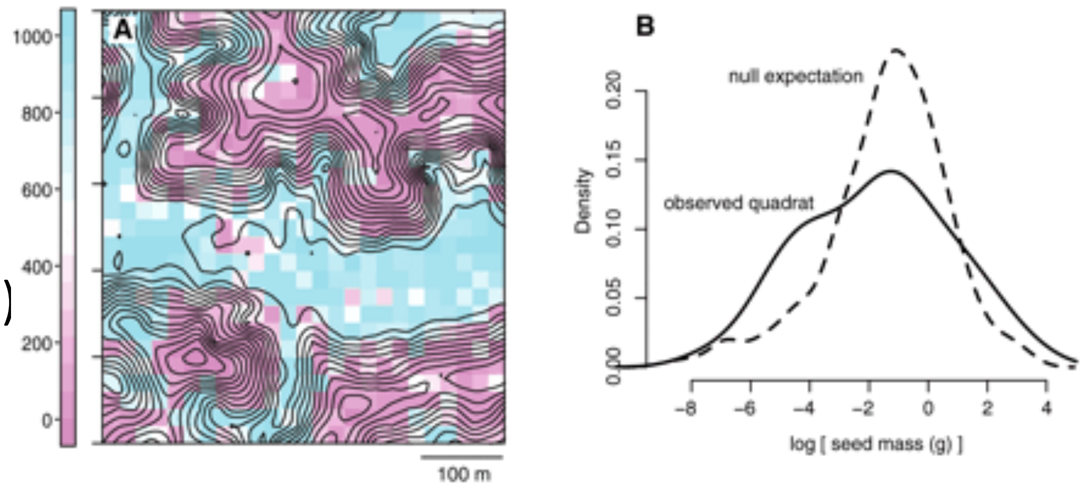
- Quantified specific leaf area (SLA, leaf area divided by dry mass), leaf nitrogen concentration, leaf size, seed mass, maximum dbh (a proxy for max height)

Paradox of the Trees

Yasuni National Park - Ecuador

Strong evidence for niche-based processes throughout the plot:

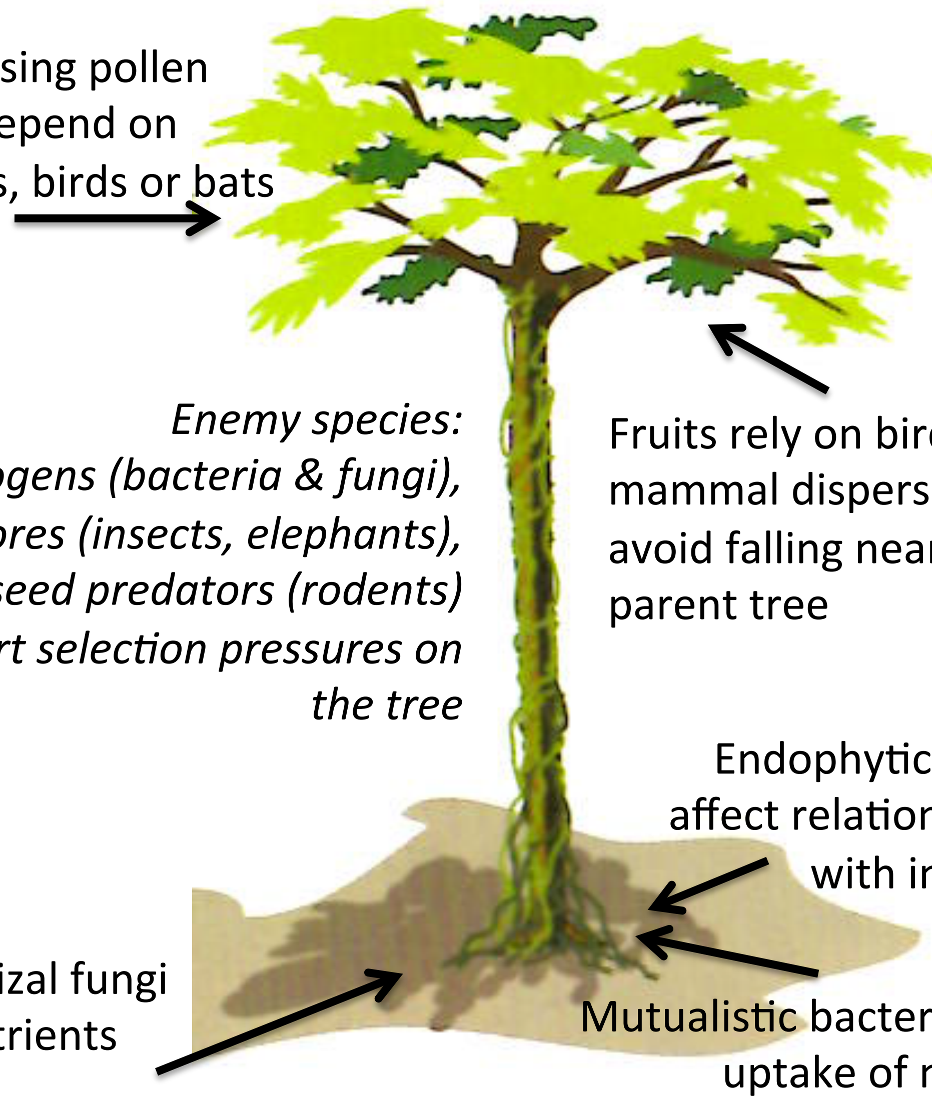
Ranges of trait values for species were small within quadrats (suggestive of strong habitat filters)



Most measured traits were more evenly distributed than expected under a null model (suggestive of high niche partitioning)

Species with a broad distribution of trait values co-occur more often than predicted.

When is a tree more than a tree?



How is such high diversity maintained in tropical forests?

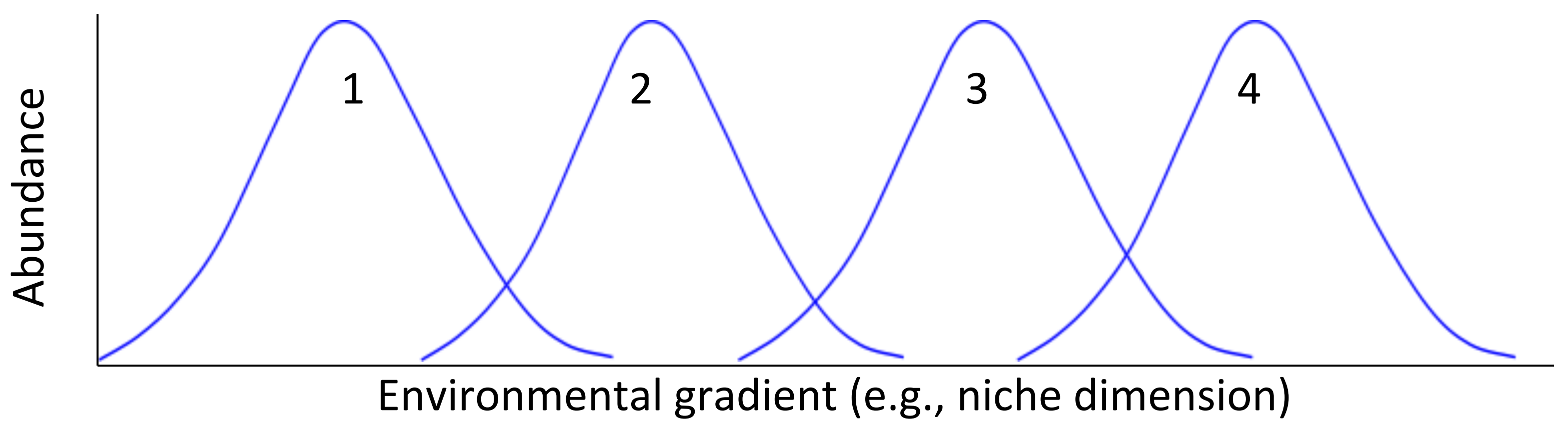
Plant ecologists have offered several hypotheses to account for the hyper-diversity of lowland forest tree communities:

- Niche-partitioning hypothesis
- Storage effects hypothesis
- Intermediate disturbance hypothesis (IDH)
- Niche complementarity hypothesis
- Negative density dependence
- Pathogen-herbivore-predator hypothesis
- Unified neutral theory (UNT)

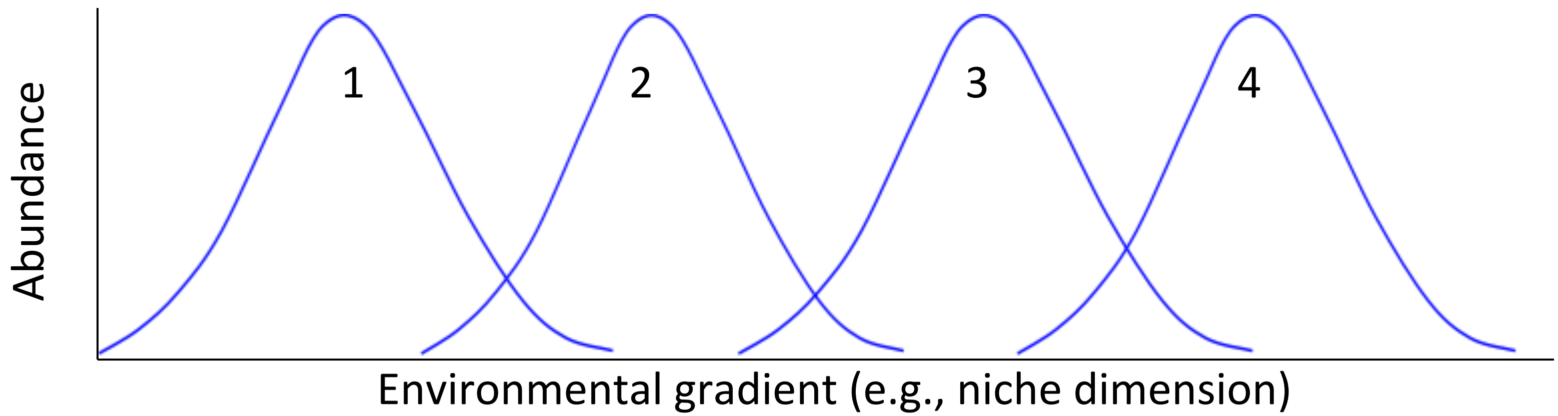
Niche-partitioning hypothesis

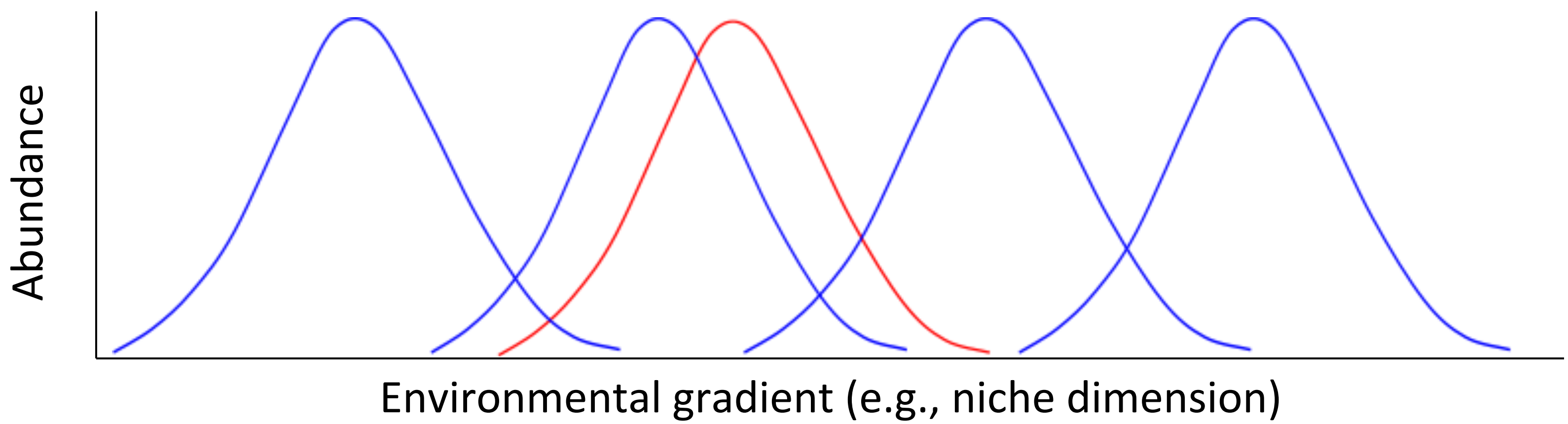
Premise: Interspecific competition forces species into increasingly narrower realized niches until each of the competing species is sufficiently specialized so that it is no longer at risk of competitive exclusion.

Example:



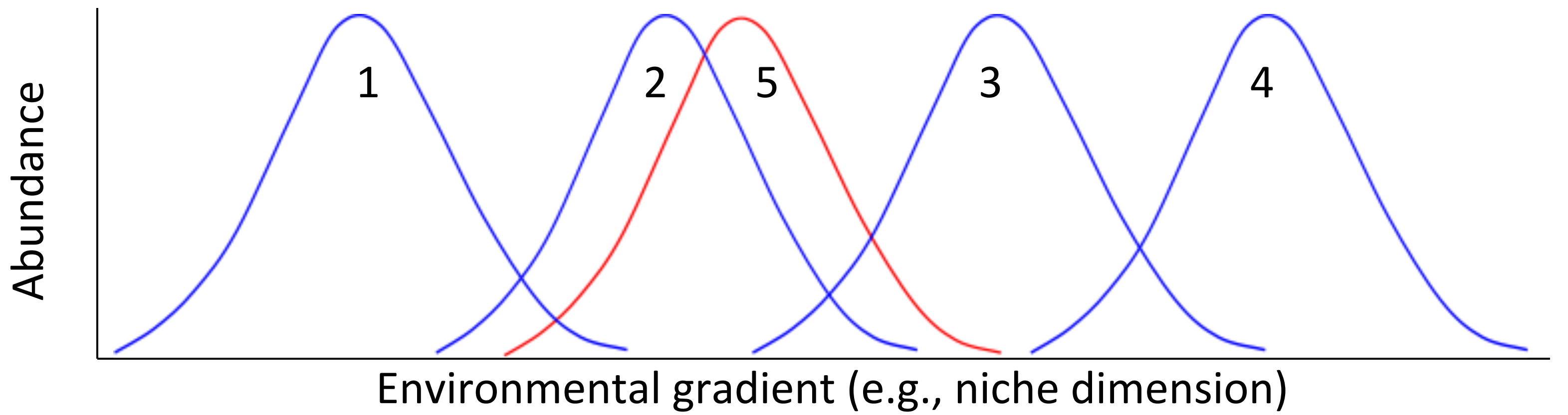
Niche-partitioning hypothesis

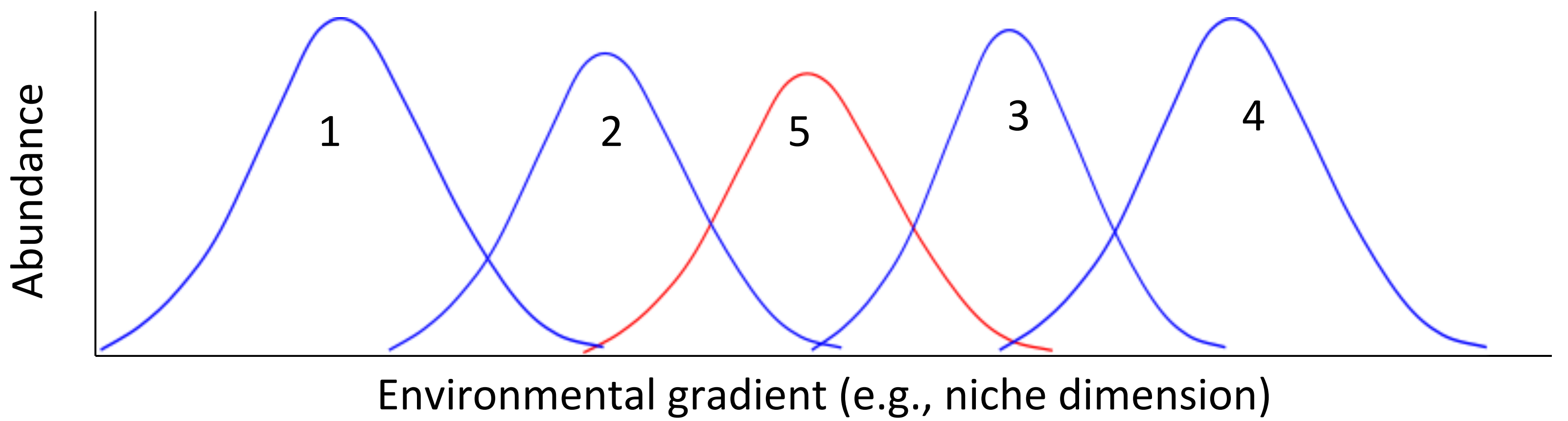




Niche theory predicts bell-shaped curves and uniformly spaced optima along gradients

Niche-partitioning hypothesis





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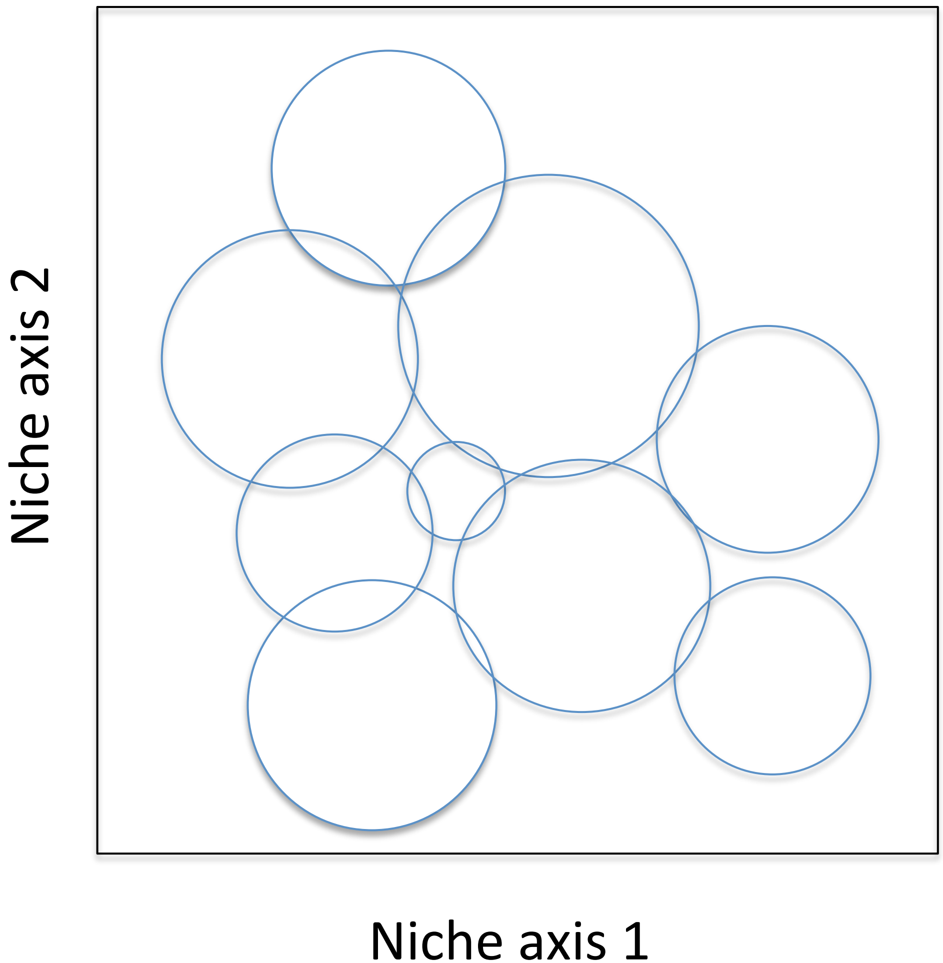
Niche-partitioning hypothesis

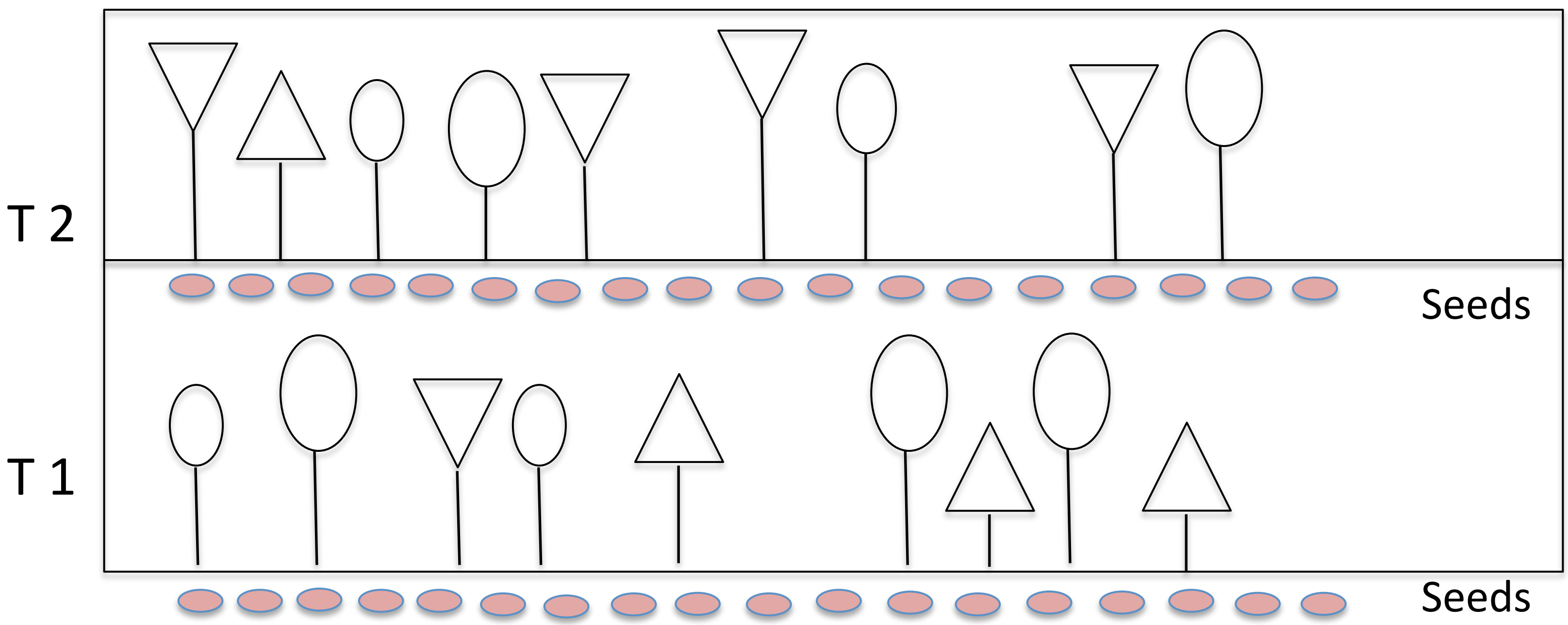


In two-dimensional niche space, species' niches attain minimal overlap

Still, how can we demonstrate how niche axes are partitioned to such a fine degree to permit existence of >300 species per hectare?

Storage effects hypothesis

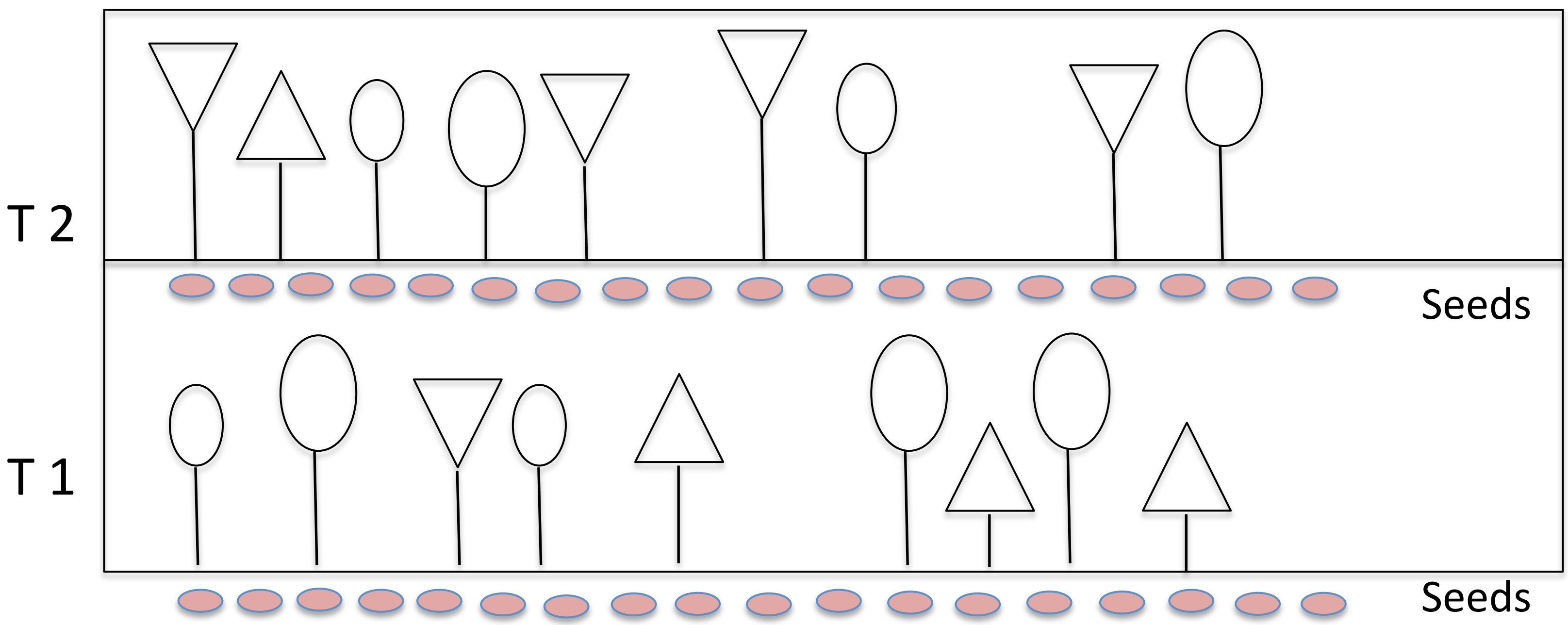
Premise: Seeds can be stored in the ground (the seed bed) for prolonged time periods, and adult trees can have high longevity (i.e., lots of opportunities to reproduce even with years of no reproductive success)



The same richness at T1 and T2 but different mixtures of species

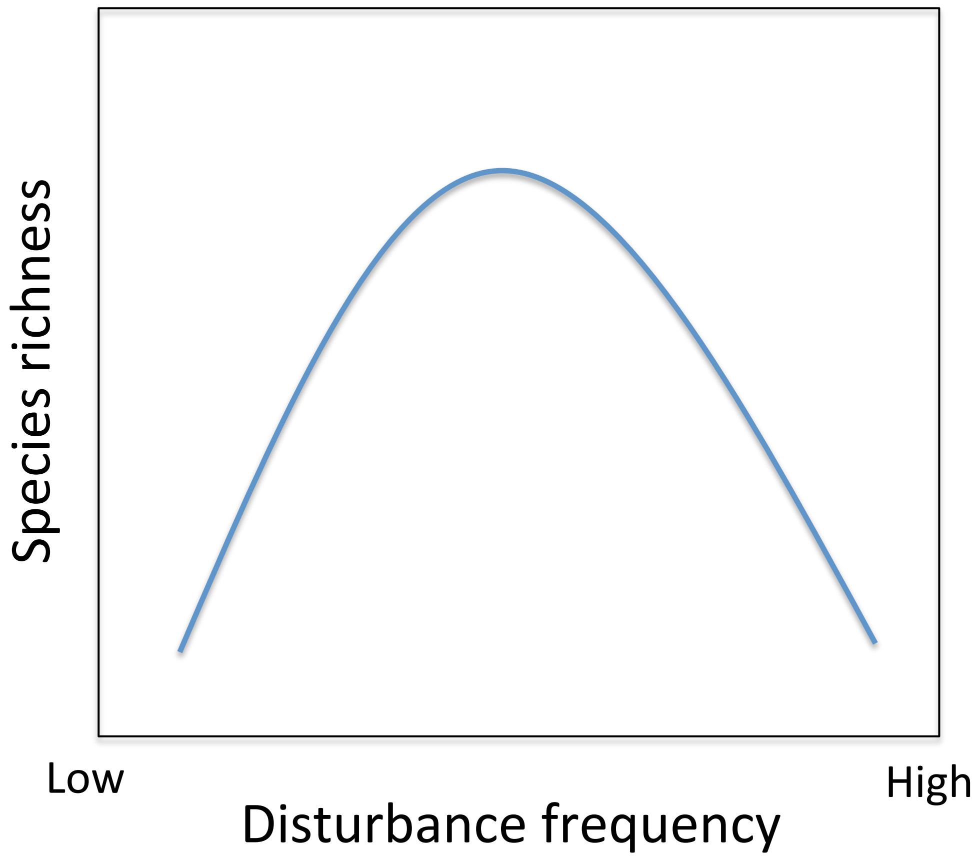
Storage effects hypothesis

Tree species can be buffered form the severe effects of competition by 'waiting it out.' Temporal variability will favor some species some of the time and others at other times – coexistence is achieved without reaching any meaningful equilibrium – composition changes by a lottery process.



The same richness at T1 and T2 but different mixtures of species

Intermediate disturbance hypothesis



Species richness is highest when disturbance frequency is intermediate

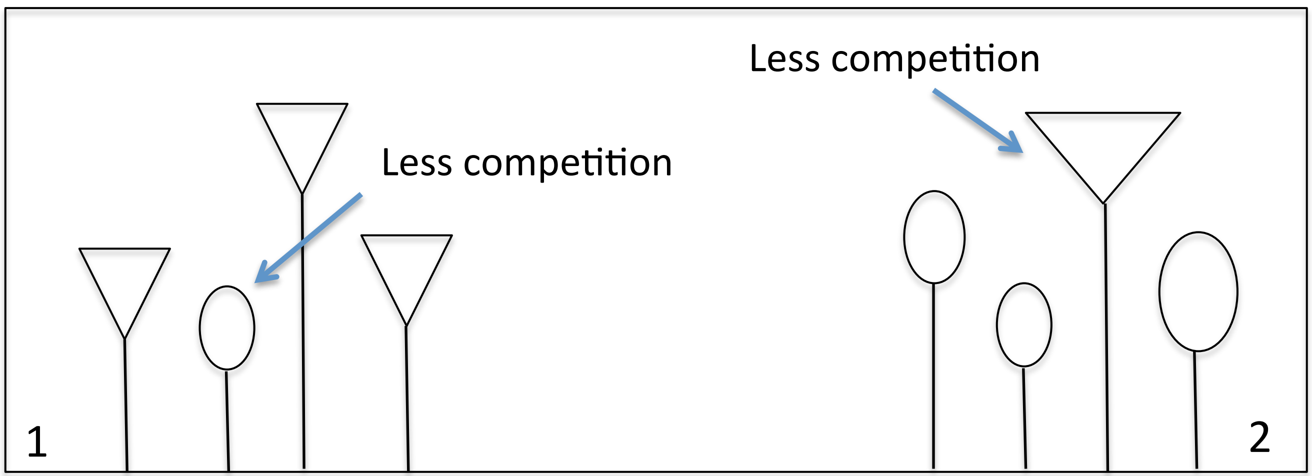
Too much disturbance reduces diversity
(few species can persist)

Too little disturbance results in lower diversity due to competitive exclusion

Forest diversity is maintained in a dynamic long-term state of non-equilibrium with species added and lost by disturbance

Frequency-dependent hypotheses

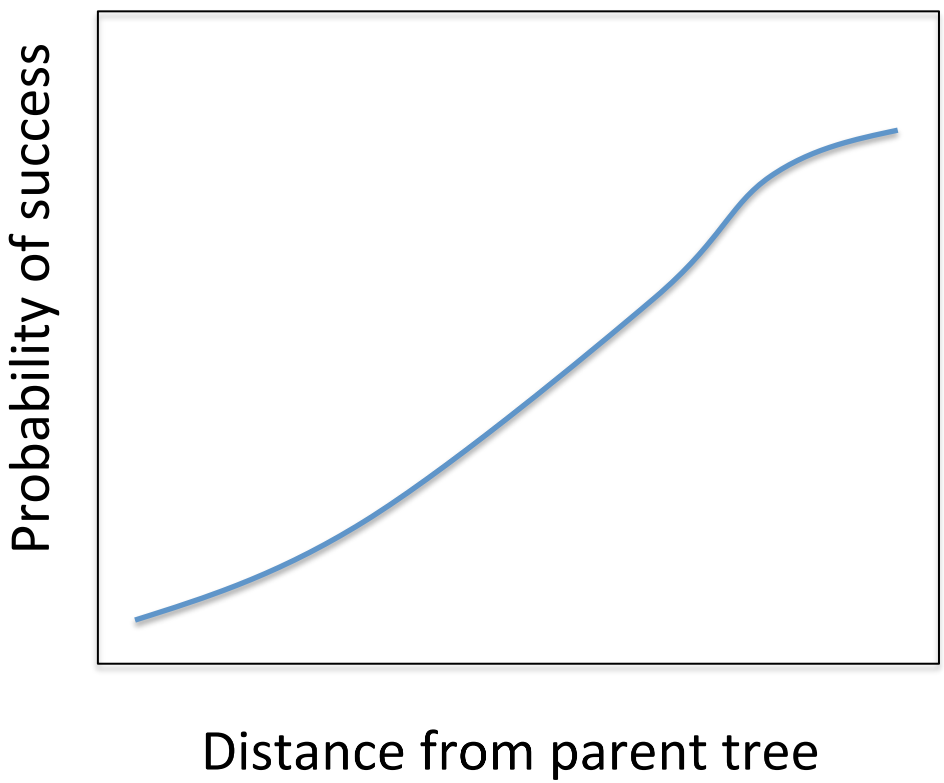
Niche-complementarity hypothesis – rare species are favored because they experience less competition than more abundance species (gain a competitive advantage)



Environmental heterogeneity
Rare species is favored in each habitat (1 or 2)

Frequency-dependent hypotheses

Negative density dependence model – Based on the idea that the parent tree is the strongest competitor against its own seedlings (Dan Janzen called this the 'seed shadow effect')

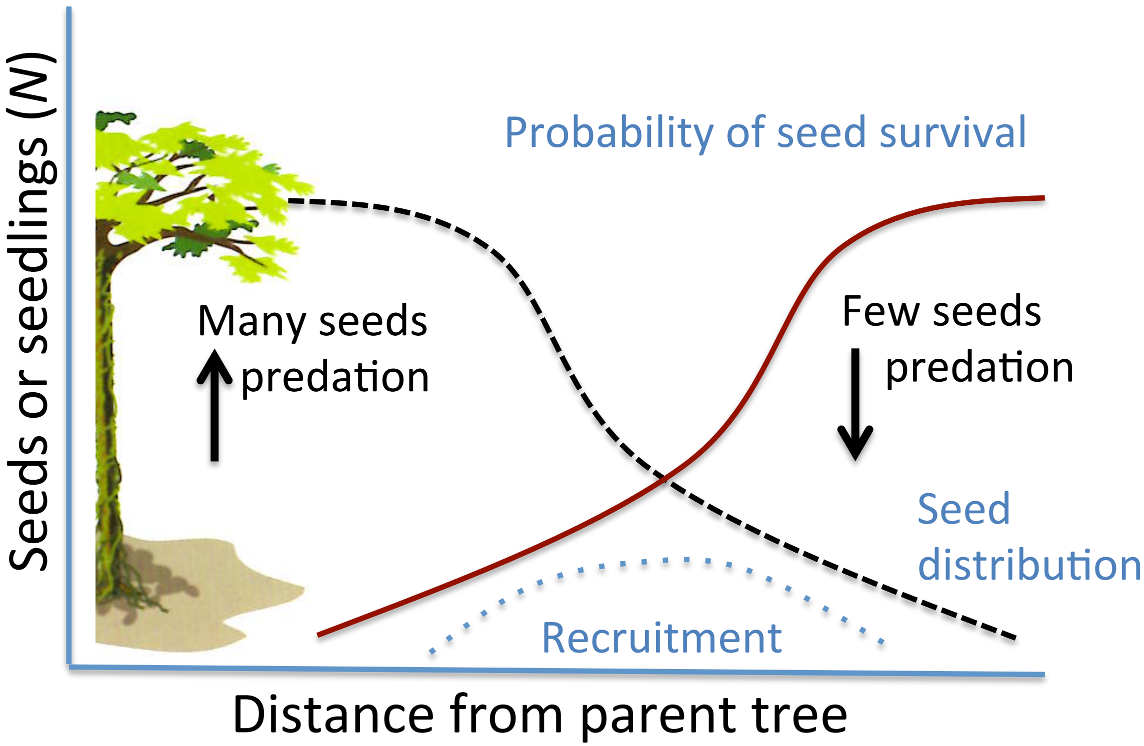


Likelihood of germination increases with distance from the parent tree

(Similar to the next hypothesis in that negative selection pressures increase with population density)

Frequency-dependent hypotheses

Pathogen-herbivore-predator hypothesis = ***Janzen-Connell hypothesis***
Diversity is maintained because of density-dependent interactions between various tree species and their pathogens/herbivores/seed predators



The most common species are bigger targets for common species

Rarer species are at a selective advantage – rarity is a defense against predation

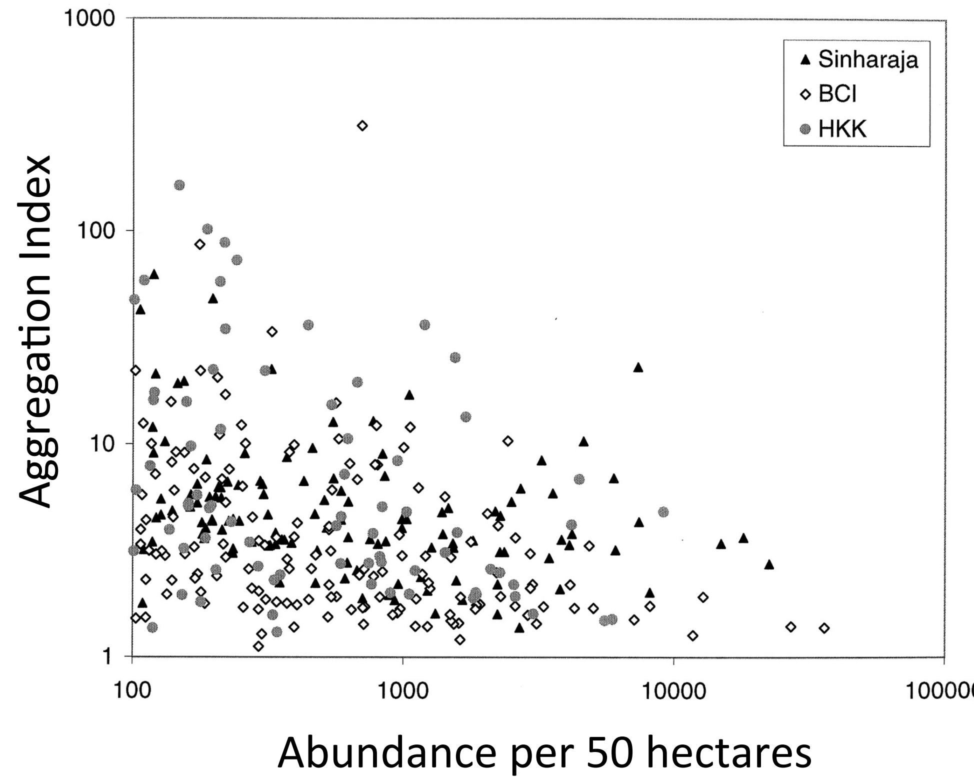
Trophic interactions are key to maintaining high tree species richness

Empirical support for some hypotheses

Global assessment of spatial distribution of species within communities

- Species aggregate within communities
- Rare species aggregate more than common species
- Aggregation was weakest in large-diameter classes

Supports hypotheses that herbivores or plant pathogens (some negative biotic interaction) act more strongly on common species, and individuals should have lower fitness close to parent tree (for common species)

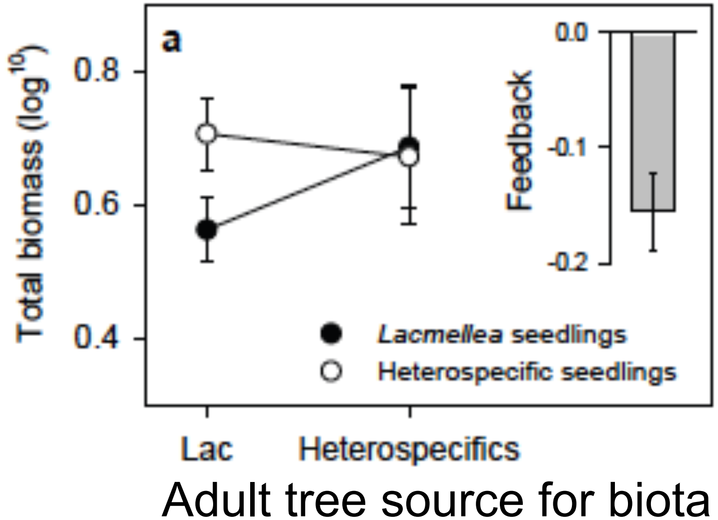


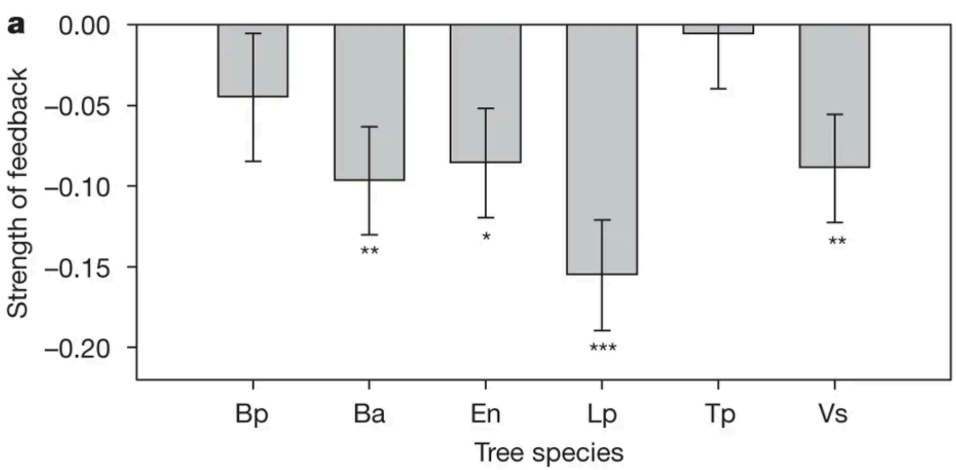
Condit et al. 2000, *Science*

Empirical support for some hypotheses

Negative density dependence: Experiment with tree seedlings

Tree species showed *negative* feedbacks when grown with their own species soil biota compared to those from heterospecifics.





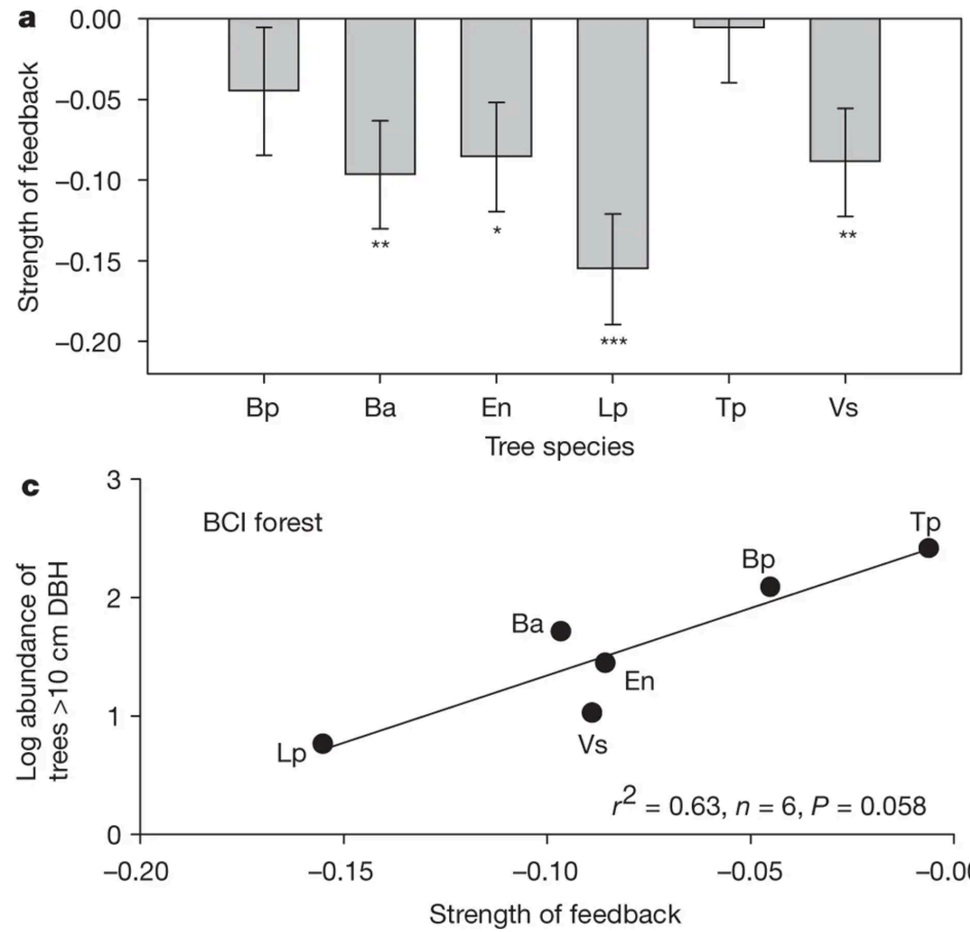
Mangan et al. 2010, *Nature*

Barro Colorado Island (BCI)

Empirical support for some hypotheses

Negative density dependence:

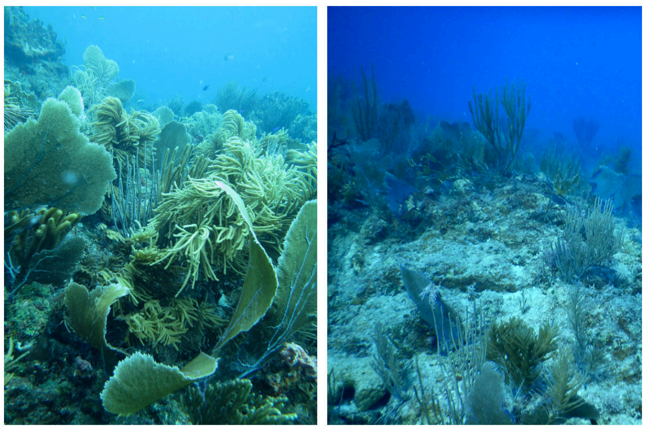
Tree species showing *stronger negative feedbacks* when grown with their own species soil biota were also less common as adults in the forest community.



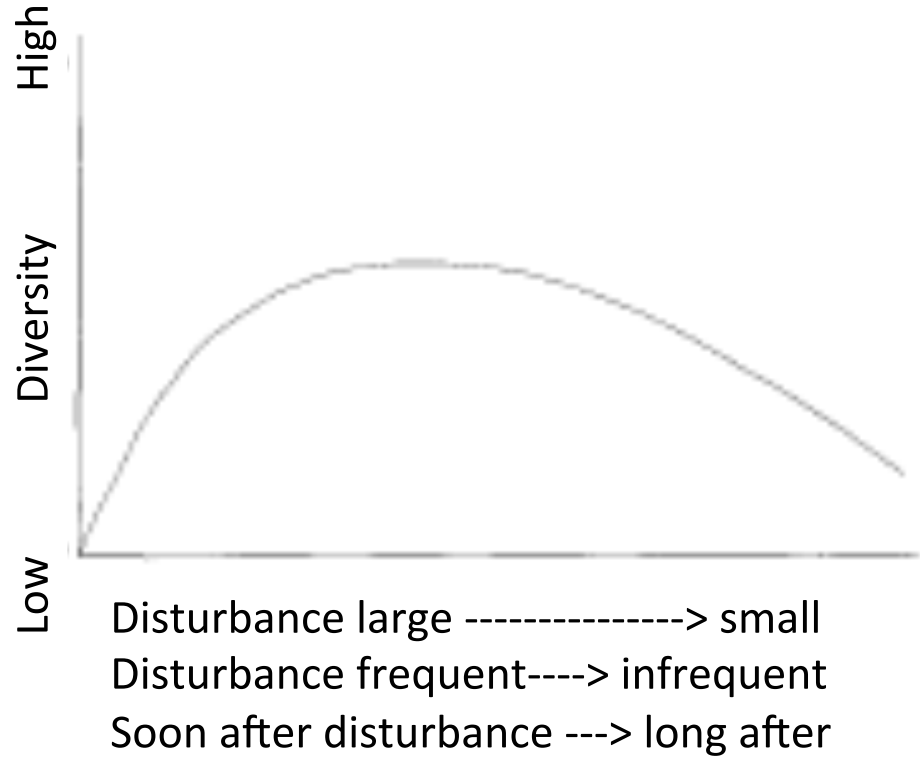
Supports hypothesis that species don't do as well when growing near conspecifics (possibly due to shared enemy pathogens). These growth patterns have implications for the abundance of adult trees, and overall patterns of diversity

IDH & Nonequilibrium communities

Under the IDH, disturbances are locally patchy, but regionally continuous.



View of coral reef in St. John, US Virgin Islands before and after hurricanes Maria & Irma



Every place is in a stage of recovery, so there is no indefinite equilibrium.

IDH helped tropical ecologists to focus on nonequilibrium forces to explain tree species richness

Unified Neutral Theory (UNT) of biodiversity and biogeography

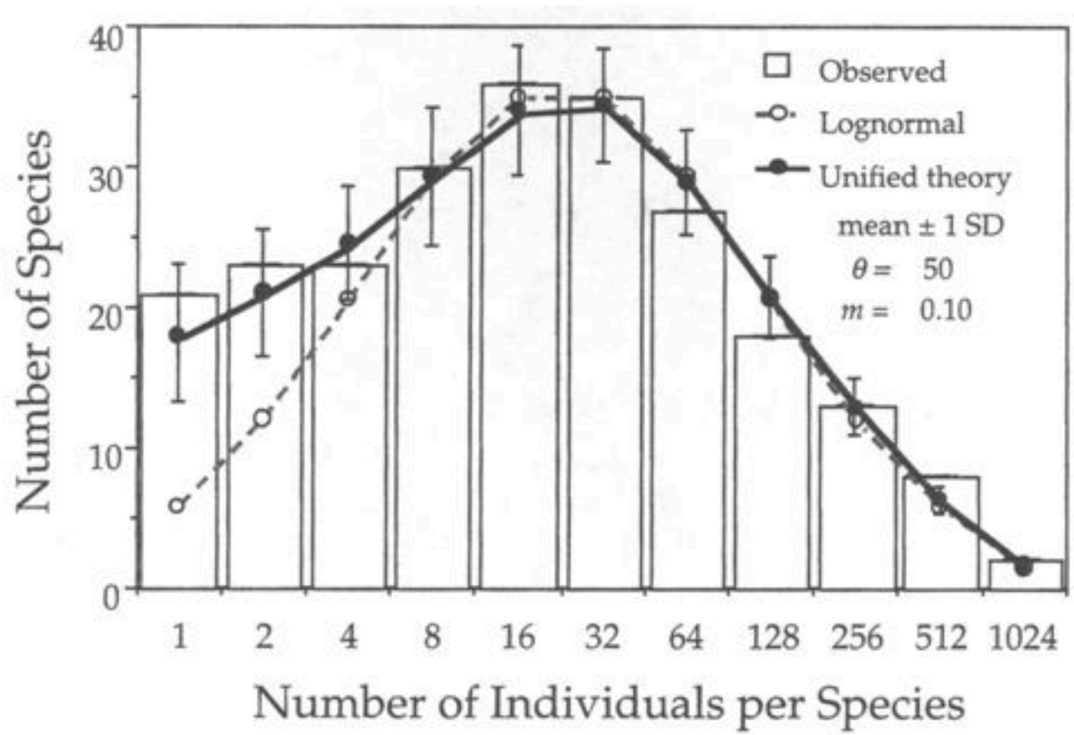
Stephen Hubbell (2001) proposed what is probably the most challenging (and controversial) hypotheses:

- *Species in a community (trees in this case) are functionally ecological equivalent (neutral in terms of interactions among individuals), and diversity can increase by nondeterministic gradual influx of species (speciation / immigration)*
- *Within an area, the number of individuals remains constant, so adding species lowers overall population densities*

When spaces open up within a community, through death of individuals, they can be replaced at random from individuals in the community, or via immigration from a larger meta-community
(zero sum ecological drift)

Unified Neutral Theory (UNT) of biodiversity and biogeography

Despite having basic assumptions that are clearly not met, the theory fits well with empirical data.



But first! Stepping back from the Unified Neutral Theory (UNT)

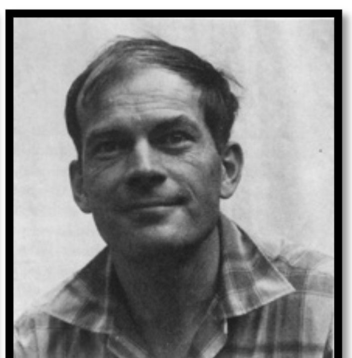
A digression with Island Biogeography:

When islands are compared with measures like species richness, two patterns emerge:

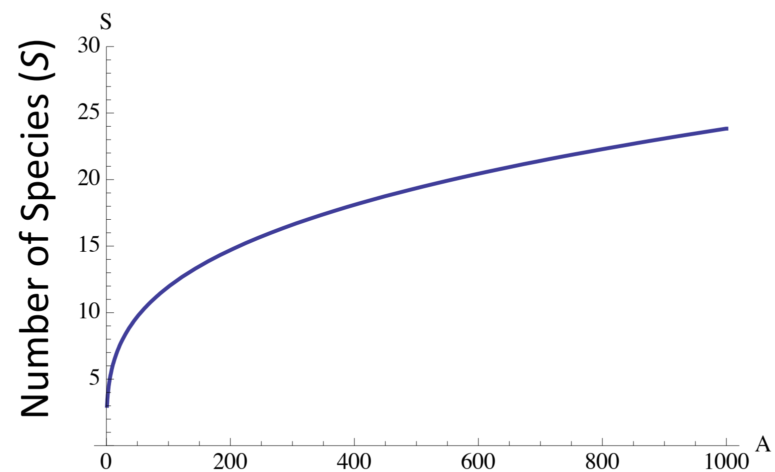
- *Species-Area effect* (larger islands hold more species than smaller ones)
- *Species-Isolation effect* (islands closer to the mainland have more species than those of equal area more isolated by distance)

E.O. Wilson

Robert MacArthur



$S = cA^z$ approximates the species - area relationship:



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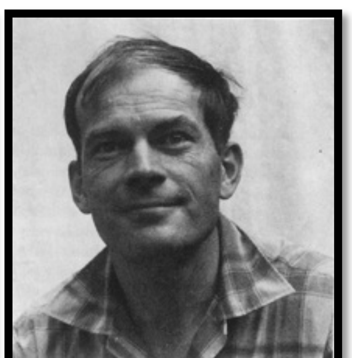

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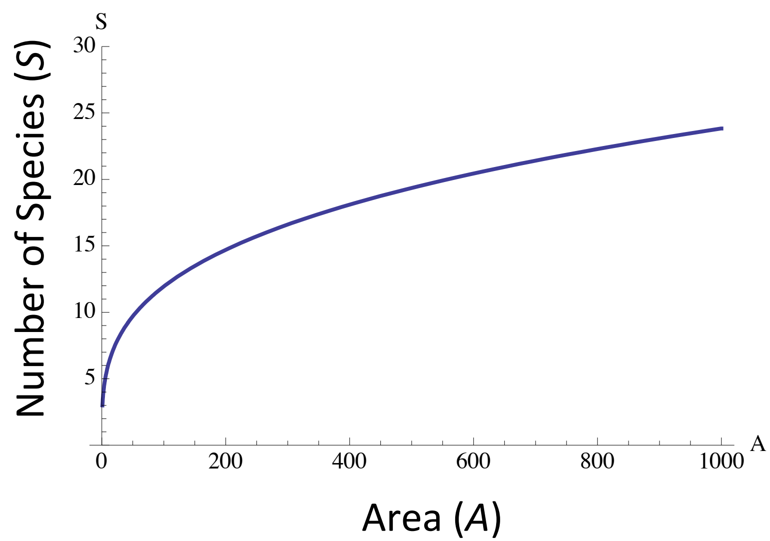


Island Biogeography: Species - Area Relationship

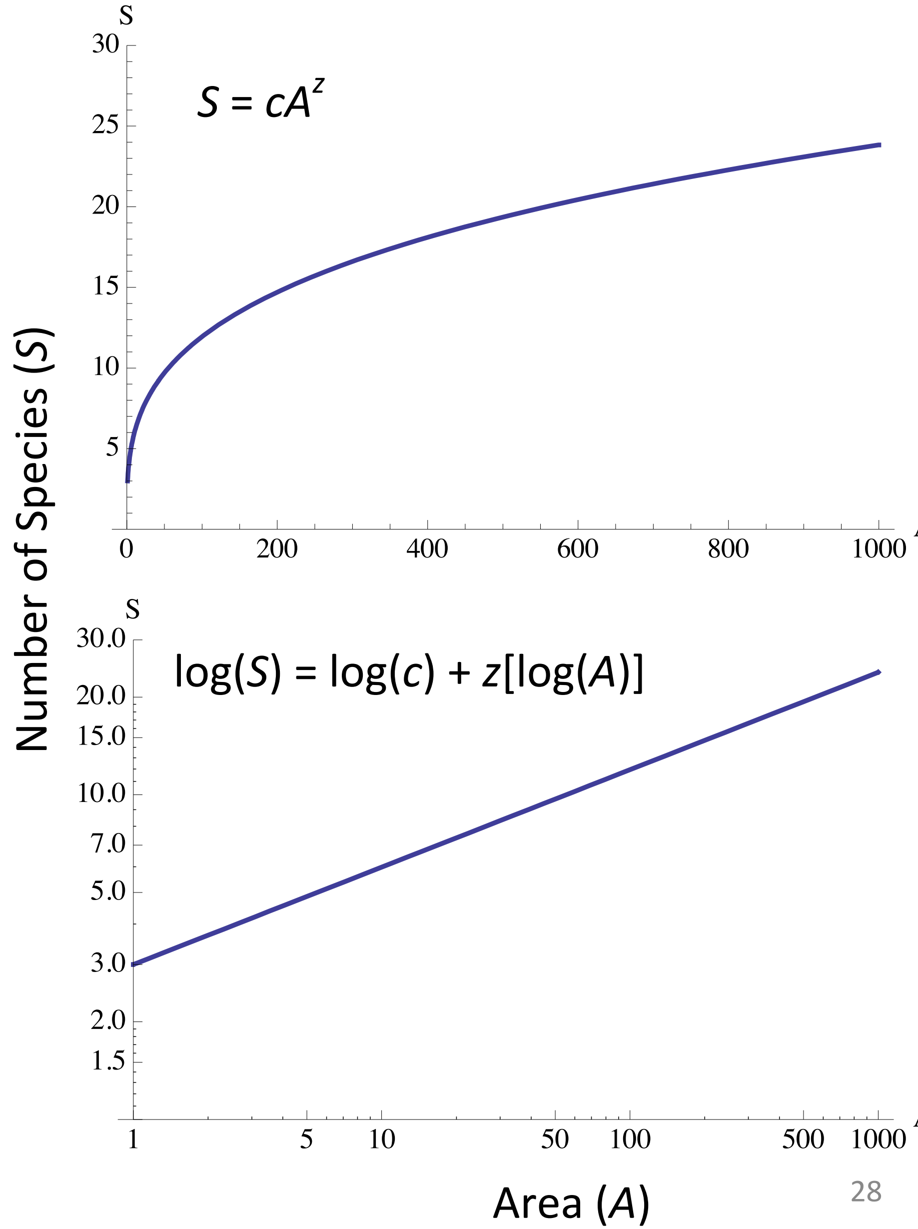
The species-area relationship is "one of community ecology's few universal regularities" - Thomas Schoener 1976

Regardless of taxonomic group or ecosystem species number tends to increase with increasing area

Species-area relationship: $S = cA^z$

S = number of species (or richness)
A = island (or habitat) area

z = fitted parameter (represents slope of the relationship when plotted on log-log scale)
c = fitted parameter (constant), but can vary substantially across islands or taxa



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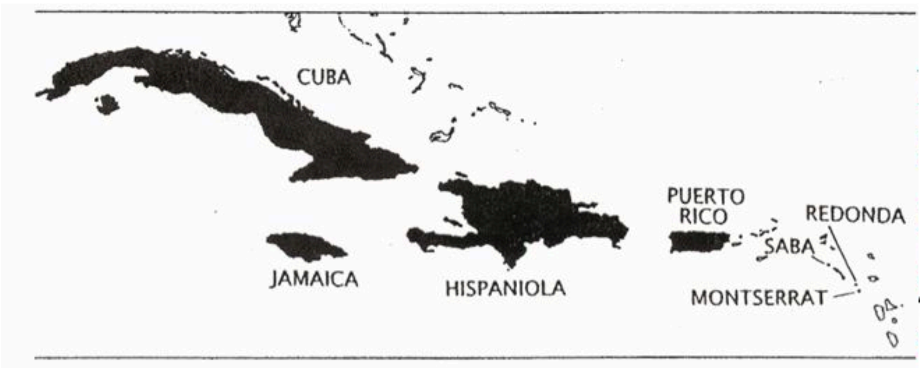
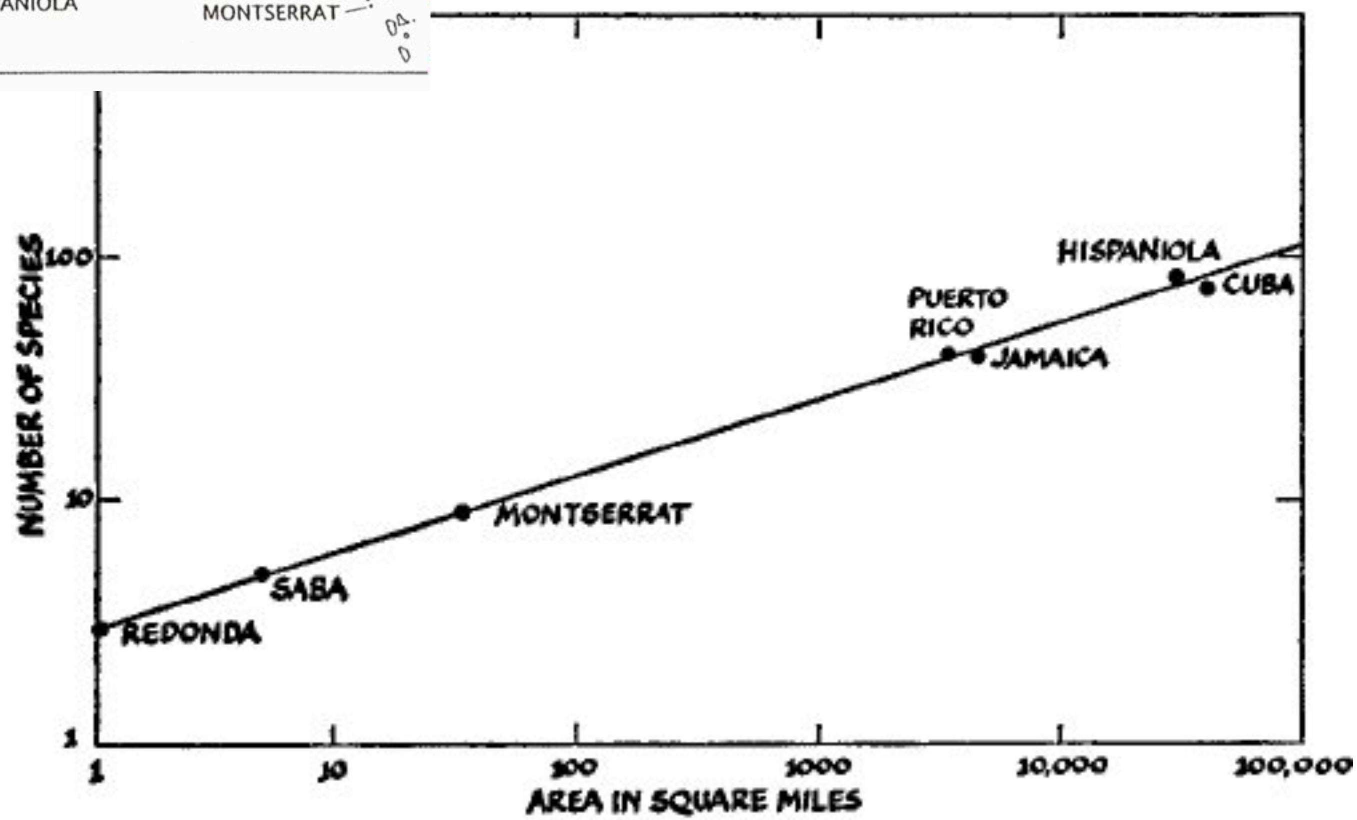


The area-species curve of the West Indian amphibians and reptiles (from MacArthur and Wilson 1967).



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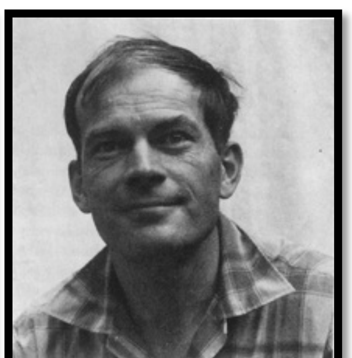
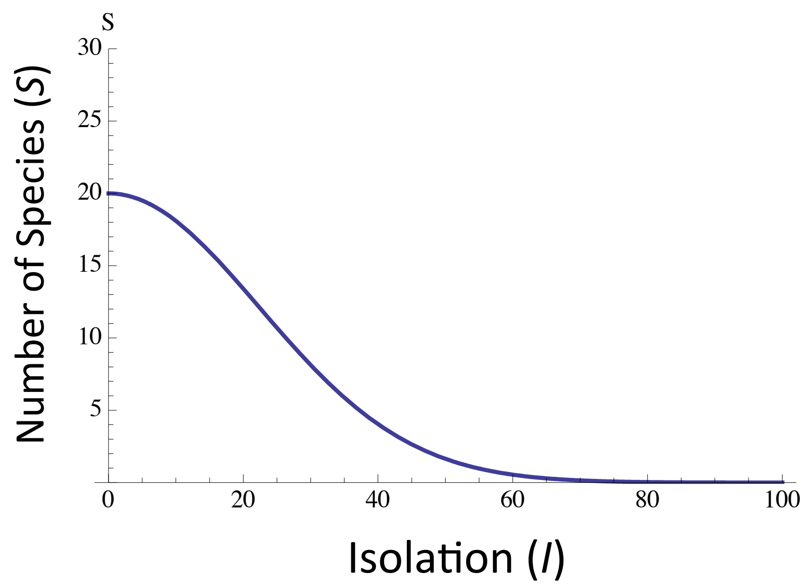


$S = k_1 e^{-k_2 (I^2)}$ approximates species - isolation relationship:



Island Biogeography: Species – Isolation Relationship

The species-isolation relationship shows a decline in richness resulting from the effect of distance on colonization rates

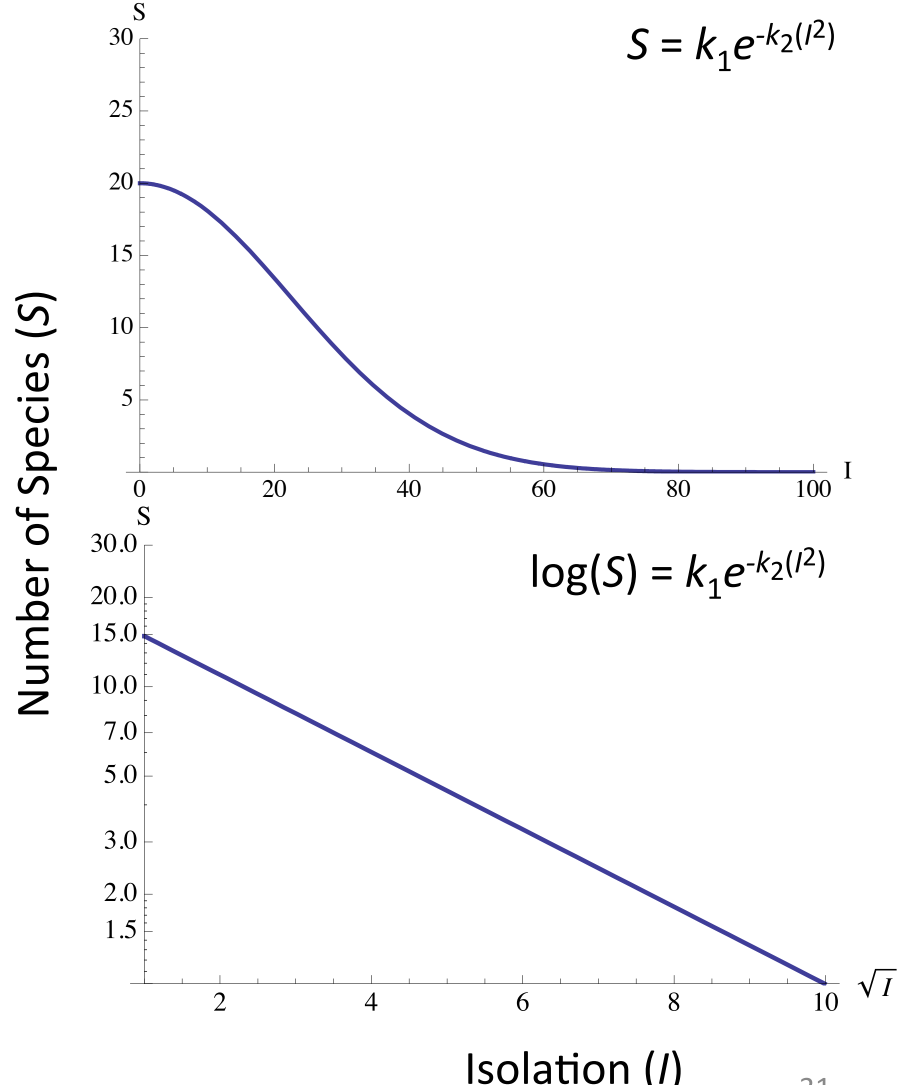
The form of the species-isolation relationship reflects the dispersal curves for the pool of species that are potential colonists from the mainland

Species-isolation relationship: $S = k_1 e^{-k_2 (I^2)}$

S = number of species (or richness)

I = isolation

k_1, k_2 = fitted constants



The Theory of Island Biogeography (MacArthur & Wilson 1967)

Islands experience both immigration and extinction of populations

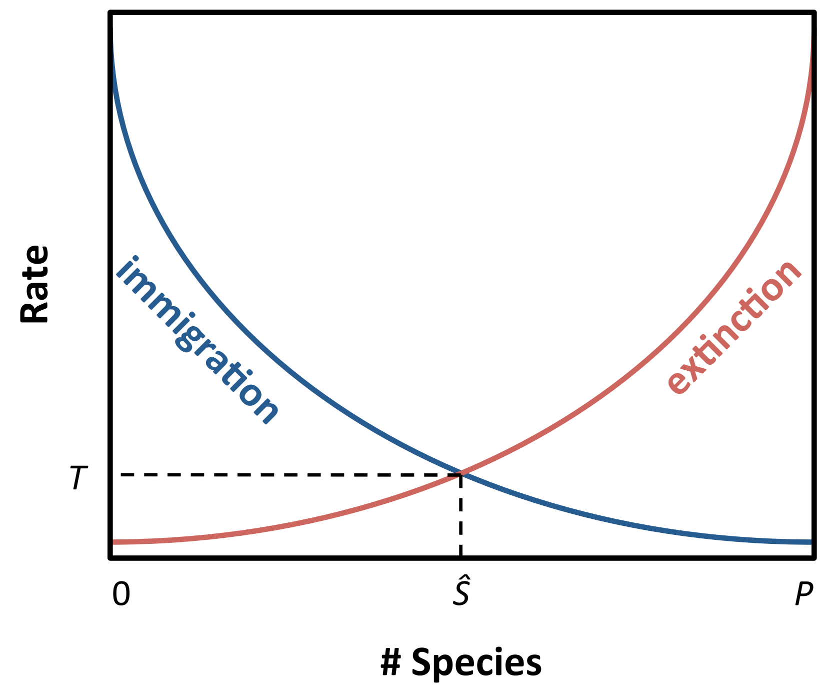
An island will eventually reach an equilibrium in *species richness*:

A barren island will experience a rate of colonization far in excess of its extinction rate.

The rate of extinction will gradually increase as species richness increases because:

- there are more species that can potentially go extinct
- negative interactions among species can increase extinction rate per species

The rate of colonization will decrease as more and more likely colonists arrive on the island



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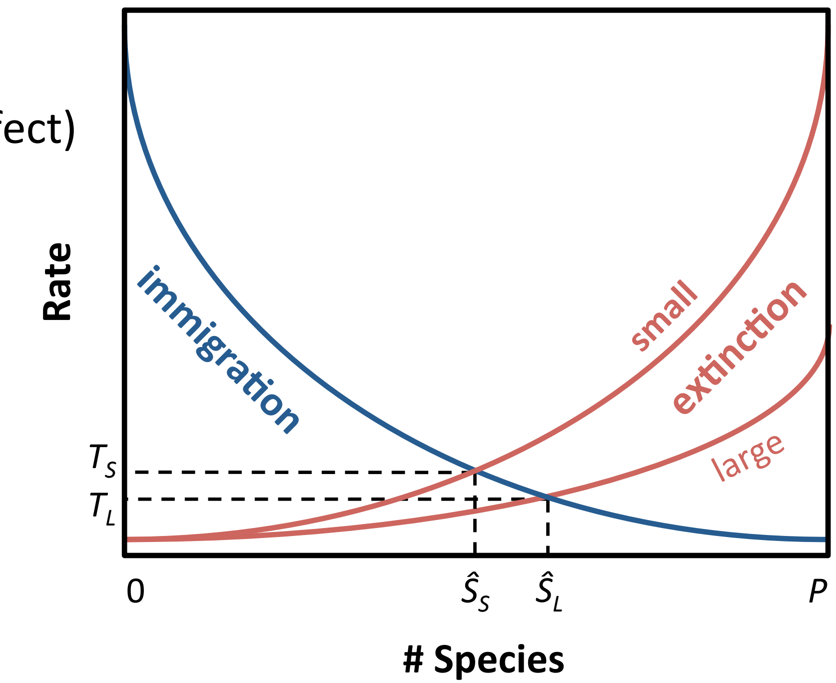
We expect islands near the mainland to have more species than far away islands (due to the species – isolation effect)



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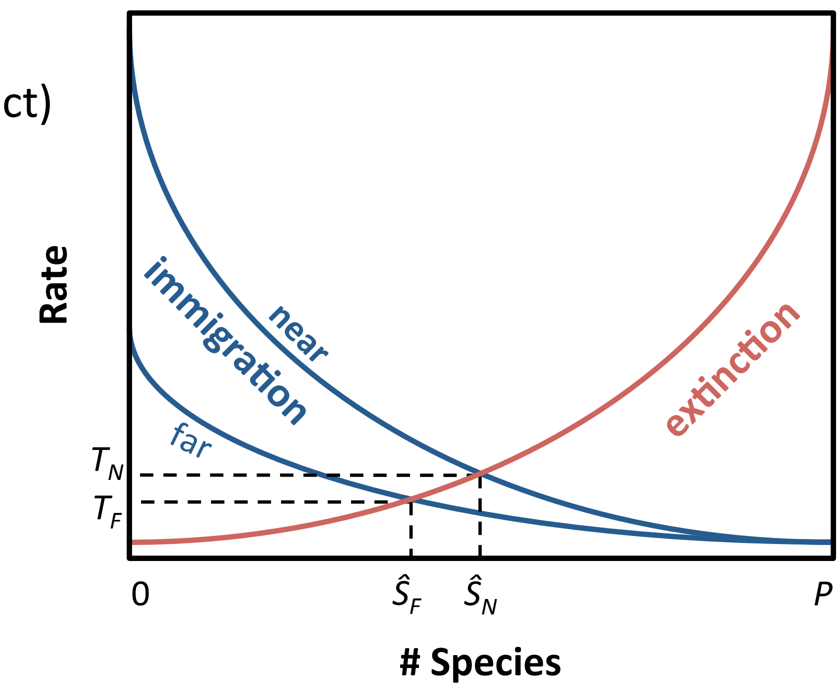


The Theory of Island Biogeography (MacArthur & Wilson 1967)

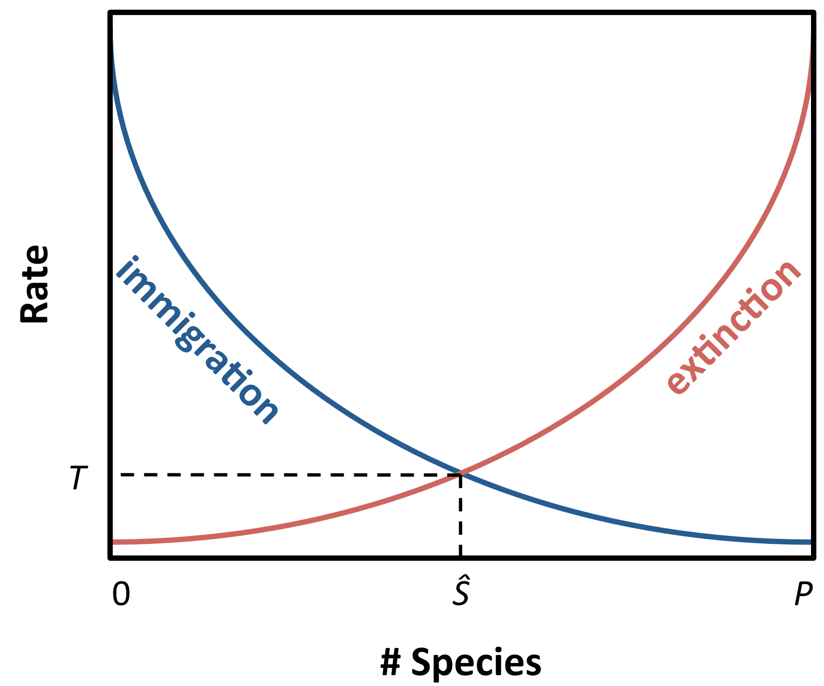
Islands will attain an equilibrium number of species for any given taxonomic group

Important notes:

The equilibrium is *dynamic* – there are ongoing immigrations and extinctions, so there is species turnover, but number of species remains constant once equilibrium is attained

The process of colonization and extinction is *stochastic* (subject to chance events)

Applies to all sorts of "islands" - allowed extensions into conservation biology

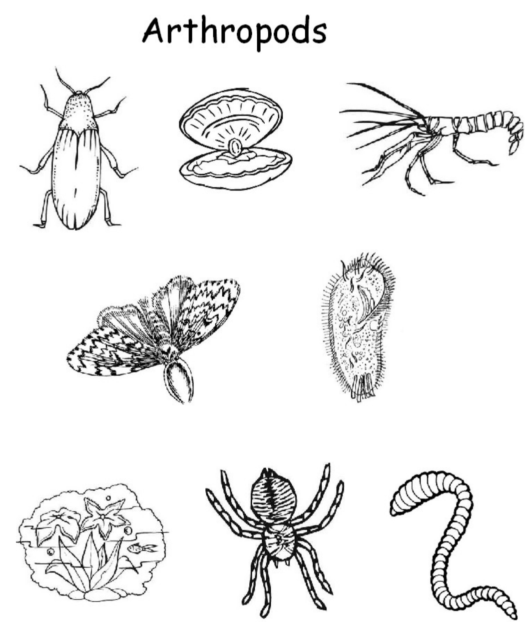


In the equilibrium theory of island biogeography, species are functionally equivalent. There are no predictions for which species will occur at the point of equilibrium, and the identity or niche differences among species do not matter in the model.

How has the theory been tested?

Defaunation experiment by Dan Simberloff and E.O. Wilson (1970)

Small islands of red mangrove in the Florida Keys (varying in area from 75-250 m^2) were surveyed for terrestrial arthropods, then covered in plastic tents and fumigated with methyl bromide to remove all arthropods. Islands varied in distance from the mainland source fauna (300 species) from 20 – 1200 m.



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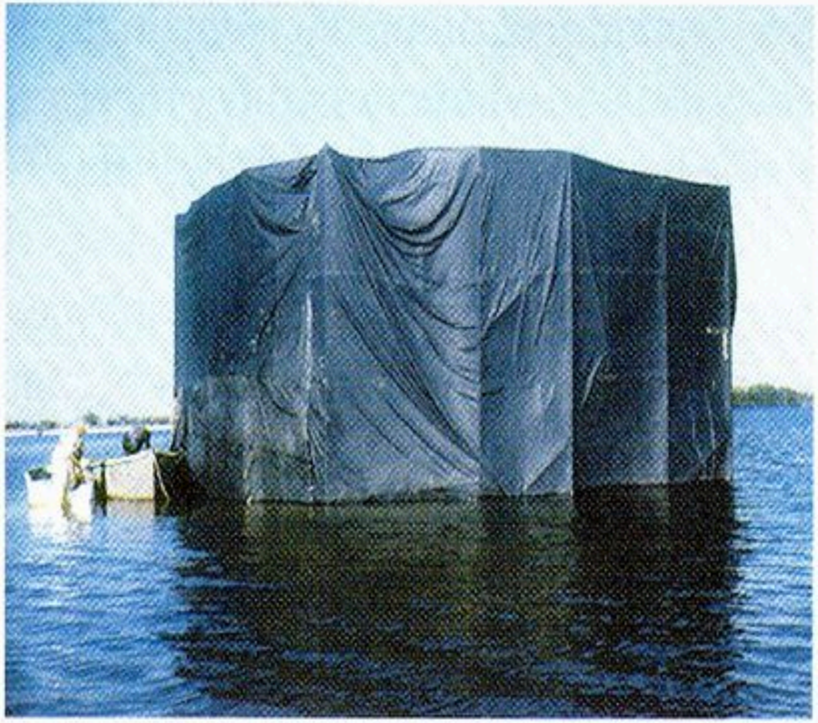
(a)



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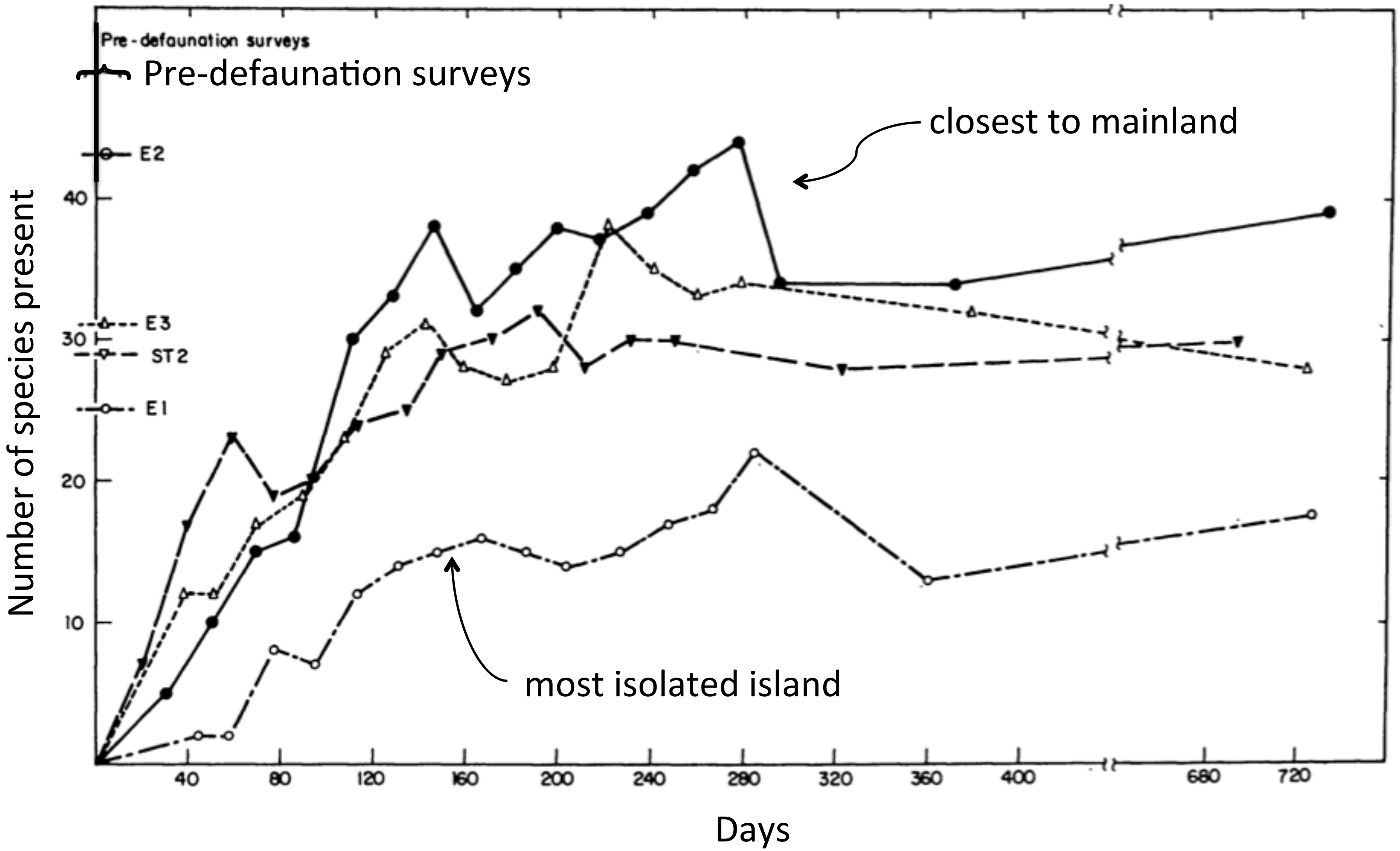

Colonization curves of four small mangrove islands (E1, E2, E3, ST2) in Florida Keys following extermination of arthropod faunas by fumigation (Simberloff and Wilson 1970)

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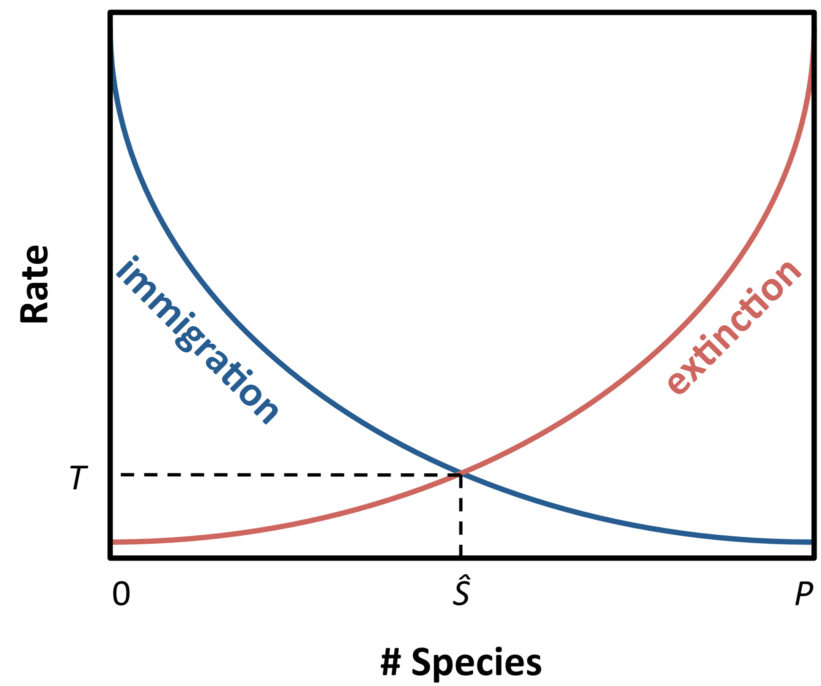
YET! *Island biogeography theory suggested to ecologists that systems are structured by "assembly rules" that determine the pattern of colonization and how equilibrium is reached…*

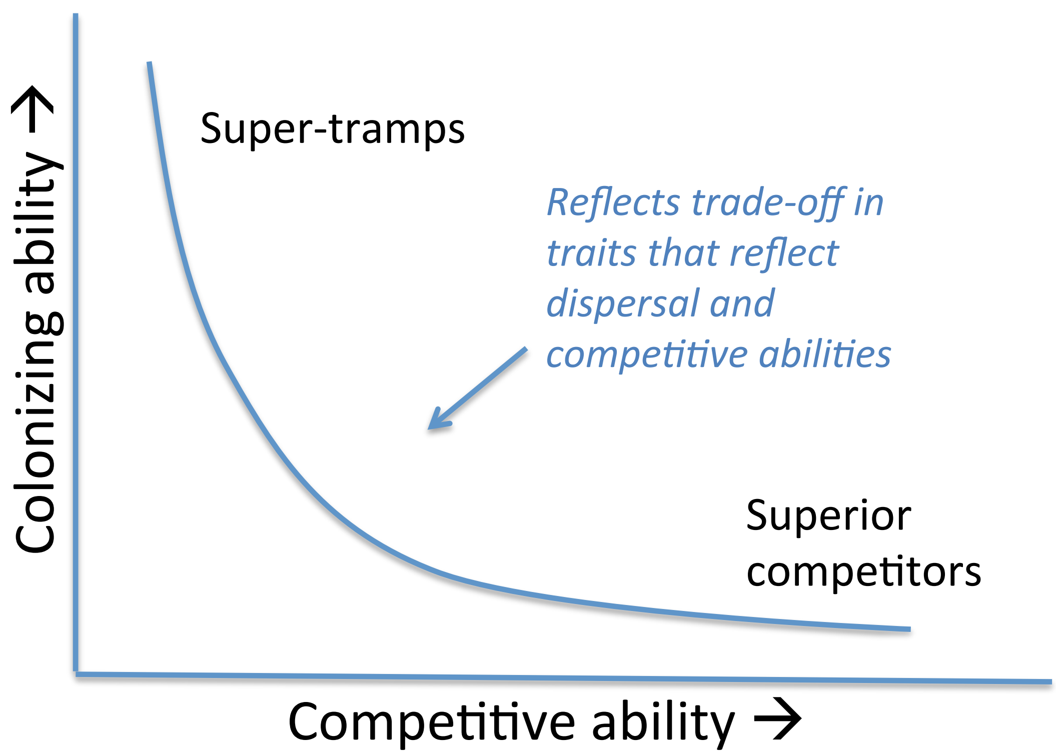
Are assembly rules important?



Assembly "rules"

Species have different adaptations for dispersal and colonization

This should affect which species occur first following a disturbance (i.e., good colonizers) followed by those with lower dispersal rates, until a community is assembled.



The patterns of colonization followed by increased species richness represent **assembly rules**

'Tramps' are the best colonists but only persist if there are few species on the island

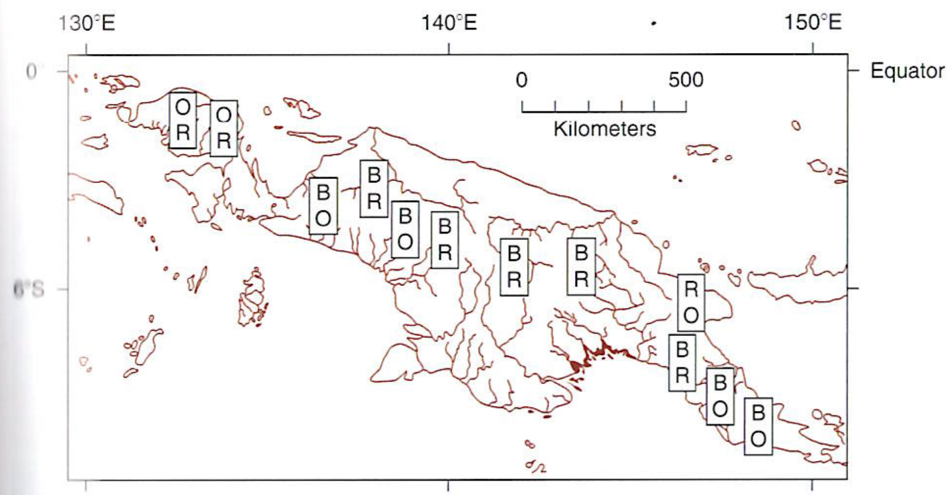
'High-S Species' are poor colonizers, but fared well in species-rich communities

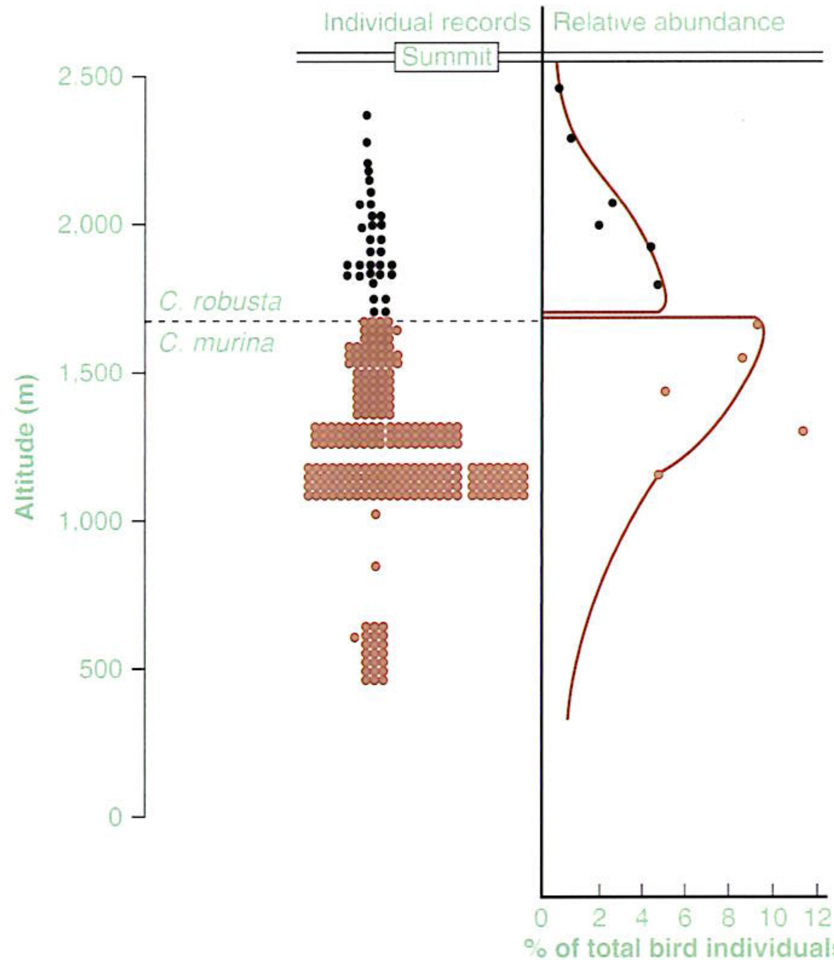
Assembly "rules"

Once more species accumulate, we expect biotic interactions to direct the assembly of communities

Are there combinations of species that are permitted or forbidden?

Jared Diamond (1975) demonstrated checkerboard patterns (forbidden combinations of species) in honeyeaters and warblers in New Guinea



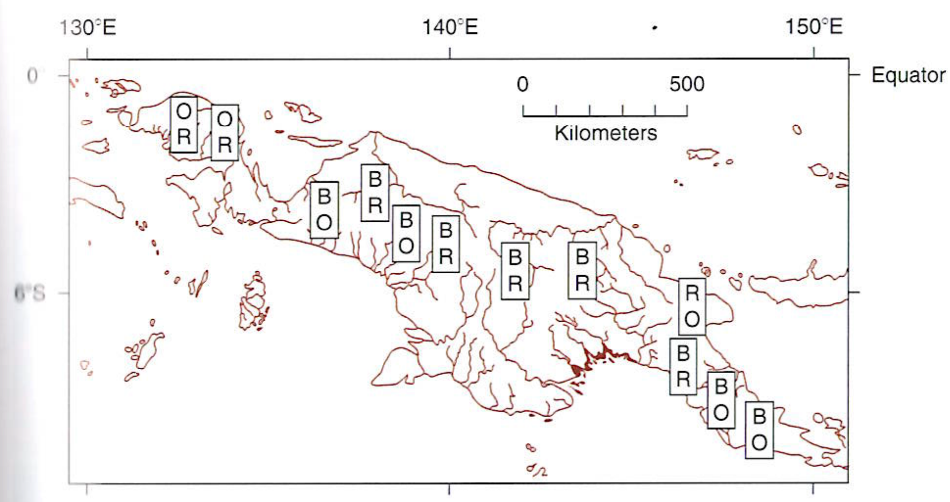


Assembly "rules" …enter Null Models

Null models have been employed to test these patterns:

What is the statistical likelihood that a particular distribution could have resulted from chance alone?

Null models offer a 'yardstick' or a statistical control to use in comparison with an observed pattern, like checkerboards



Unified Neutral Theory (UNT) of biodiversity and biogeography

Stephen Hubbell began to question how tropical tree species diversity is maintained, working on Barro Colorado Island (BCI)

- *Found that dry forest tree species were not in equilibrium*
- *Species did not divide resources to occupy separate niches*
- *Proposed that periodic disturbance could prevent competitive exclusion and allow for slow accumulation of species*

Saw the dynamics of the forest shaped by stochastic processes, not by deterministic forces like competition.

He viewed tree species as being ecologically egalitarian (subject to neutral variation in abundance)

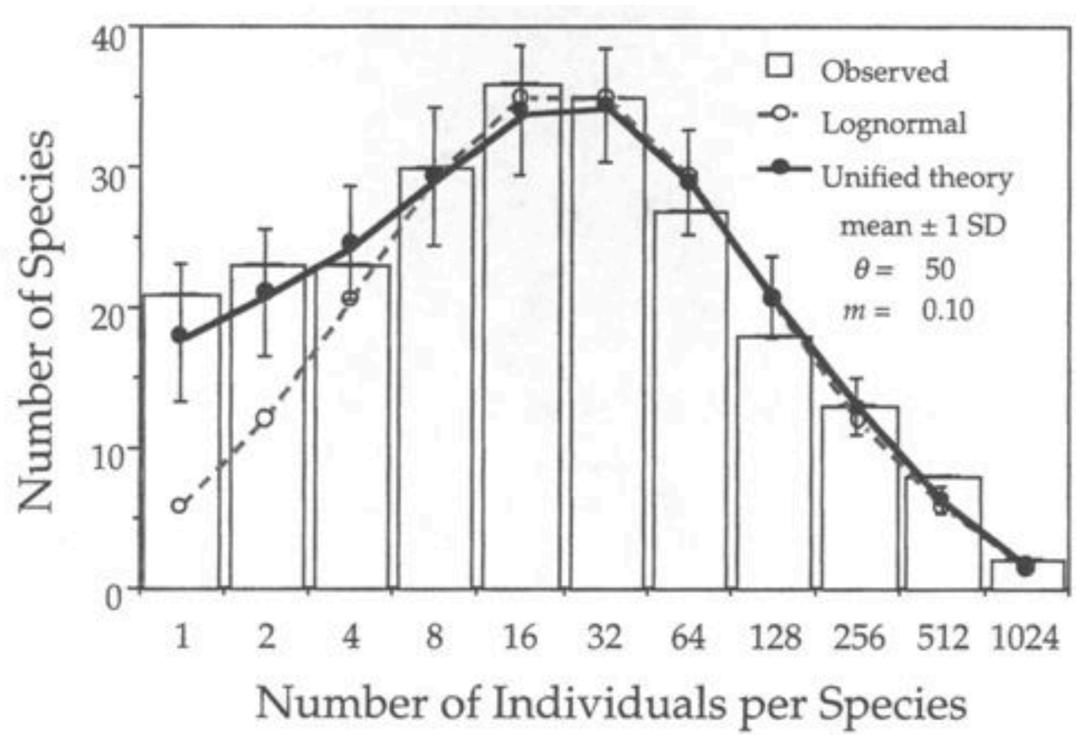
Hubbell's UNT included *speciation*, immigration and extinction to combine biogeography and biodiversity in a unified construct.

Unified Neutral Theory (UNT) of biodiversity and biogeography

Stephen Hubbell (2001) proposed the UNT:

Species in a community (trees in this case) are functionally ecological equivalent (neutral in terms of interactions among individuals), and diversity can increase by nondeterministic gradual influx of species (speciation / immigration)

Within an area, the number of individuals remains constant, so adding species lowers overall population densities



When spaces open up within a community, through death of individuals, they can be replaced at random from individuals in the community, or via immigration from a larger meta-community (zero sum ecological drift)

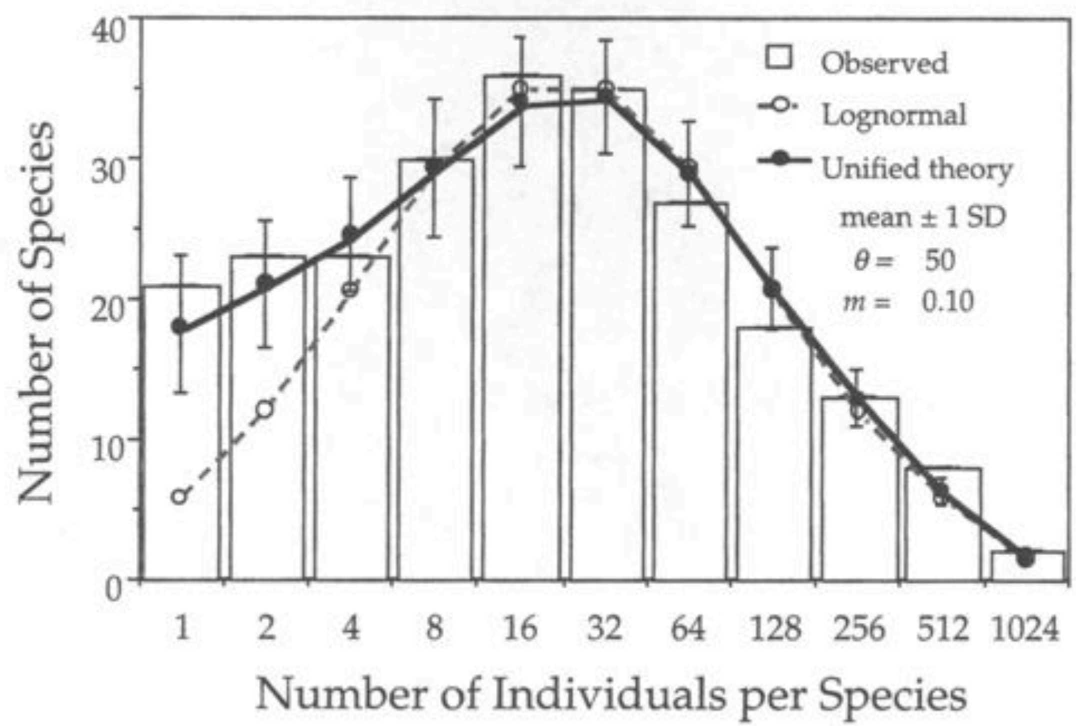
Unified Neutral Theory (UNT) of biodiversity and biogeography

Stephen Hubbell (2001) proposed the UNT:

Involves a complex mathematical model that generates a single dimensionless number

The fundamental biodiversity number theta (θ)

θ is a function of speciation rate and the size of the metacommunity, which can be used to predict the relative abundance of species in a community.



The model includes the following variables: probability of birth (*b*) and death (*d*) for each individual, probability of immigration (*m*) for each species, Number of individuals (*K*) in each community, Number of species (*N*) in the external species pool

A challenge to UNT from trees

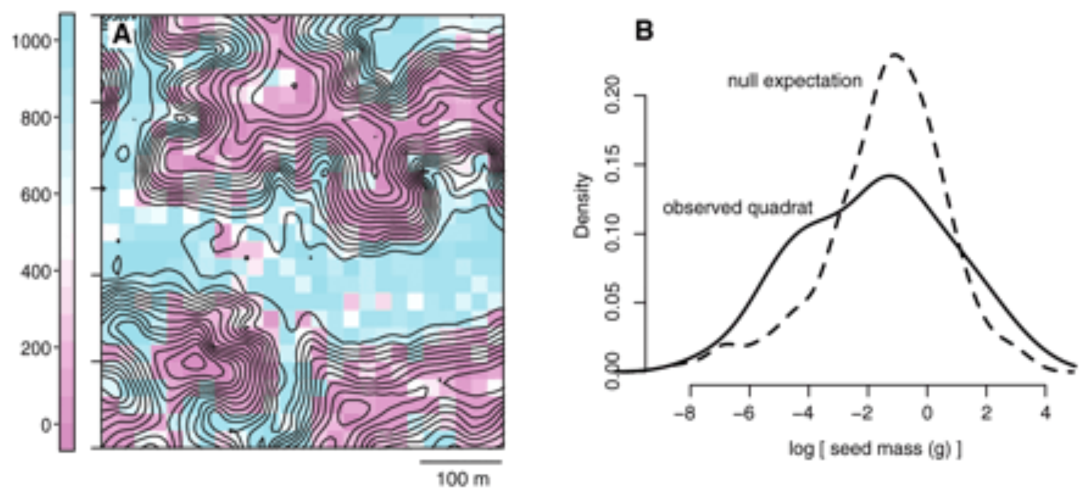
Yasuní Forest Dynamics Plot (FDP)

- 25-ha plot containing over 150,000 mapped trees ≥1 cm at DBH for over 1100 species

- Quantified specific leaf area (SLA, leaf area divided by dry mass), leaf nitrogen concentration, leaf size, seed mass, maximum dbh (a proxy for max height)

Co-occurring species converge in characteristics due to strong abiotic selection pressures (environmental filtering)

Co-occurring species diverge as predicted by classic niche differentiation theory



Species with a broad distribution of trait values co-occur more often than predicted.

A challenge to UNT from trees

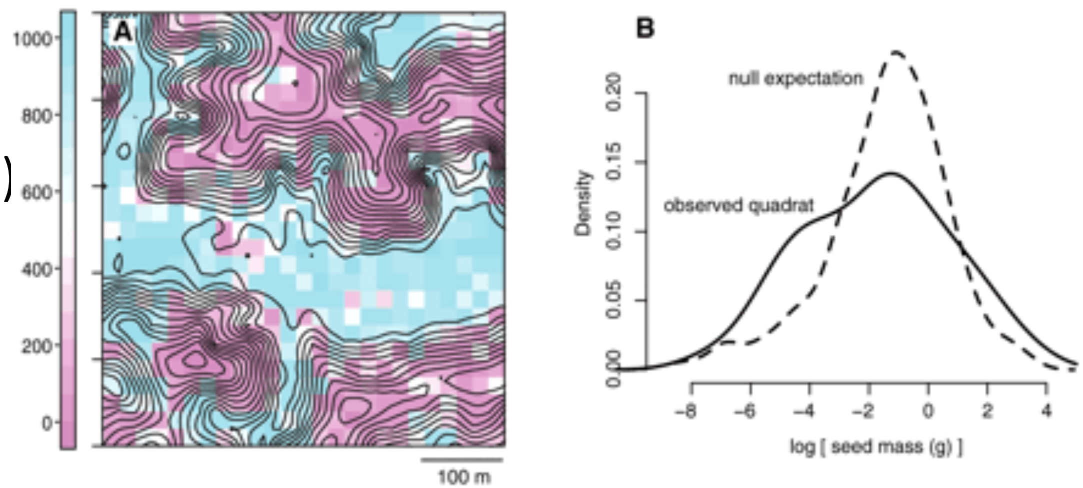
Yasuní Forest Dynamics Plot (FDP)

- 25-ha plot containing over 150,000 mapped trees ≥1 cm at DBH for over 1100 species

- Quantified specific leaf area (SLA, leaf area divided by dry mass), leaf nitrogen concentration, leaf size, seed mass, maximum dbh (a proxy for max height)

Ranges of trait values for species were small within quadrats (suggestive of strong habitat filters)

Most measured traits were more evenly distributed than expected under a null model (suggestive of high niche partitioning)



"…forces included in neutral theory (such as demographic stochasticity and dispersal limitation) may not be sufficient to explain species distributions and maintenance of diversity in this forest, even though they are occurring." – Kraft et al. 2008