

Neutrality

2023

The plan today

1. Intro to metacommunity dynamics
2. Bell's Neutral macroecology
3. Unified Neutral theory of Biodiversity
 - Drift effects on local communities...
 - ...offset by speciation and immigration from regional pool
4. Niche-neutrality

“Why are there so many kinds of animals?”

Hutchinson GE (1959) Homage to Santa-Rosalia or why are there so many kinds of animals?
American Naturalist 93: 145–159.

Lawton's dilemma or why are some patches richer than others

“For twenty years, I studied a local guild of insects feeding on a patch of bracken fern, *Pteridium aquilinum*, at Skipwith Common, Yorkshire, in northern England. Over the study period, this bracken patch held an average of just over 17 species each year, with a minimum of 15, and a maximum of 19.”

Lawton, J.H. (1999). Are there general laws in ecology?
Oikos, 84, 177-192.

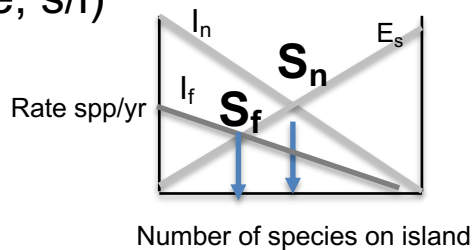
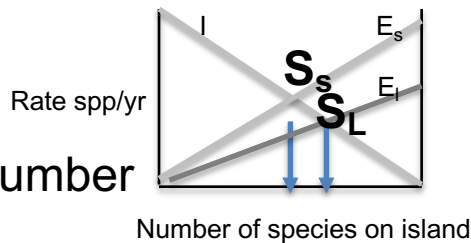
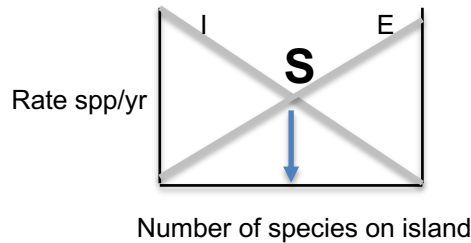


Why 17?

In crude order-of-magnitude terms, why not 2, or 170?

Island biogeography

local richness depends on persistence and distance from regional pool



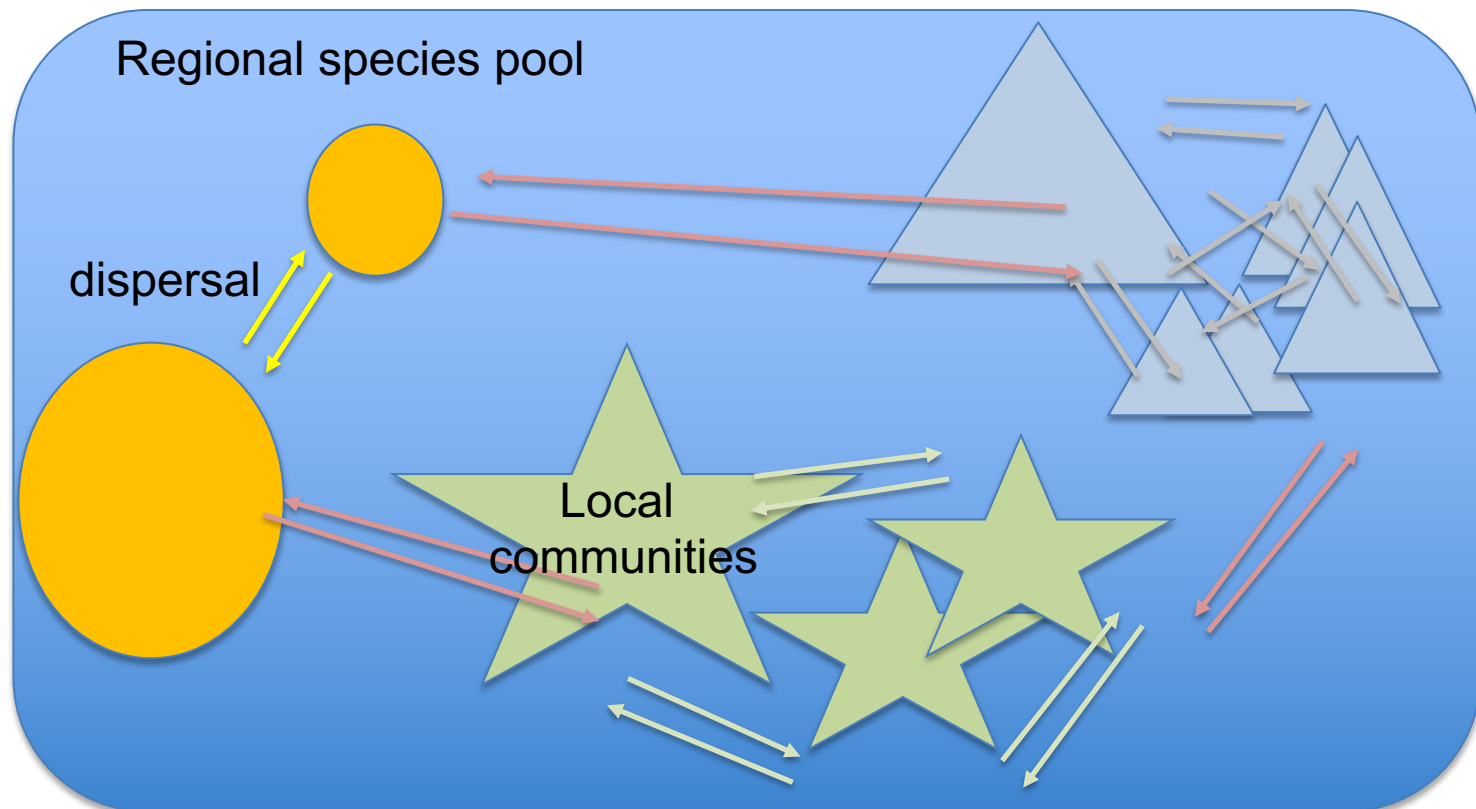
Equilibrium species number
based on:

Immigration (distance, n/f)
Extinction (island size, s/l)

1. Metacommunity dynamics

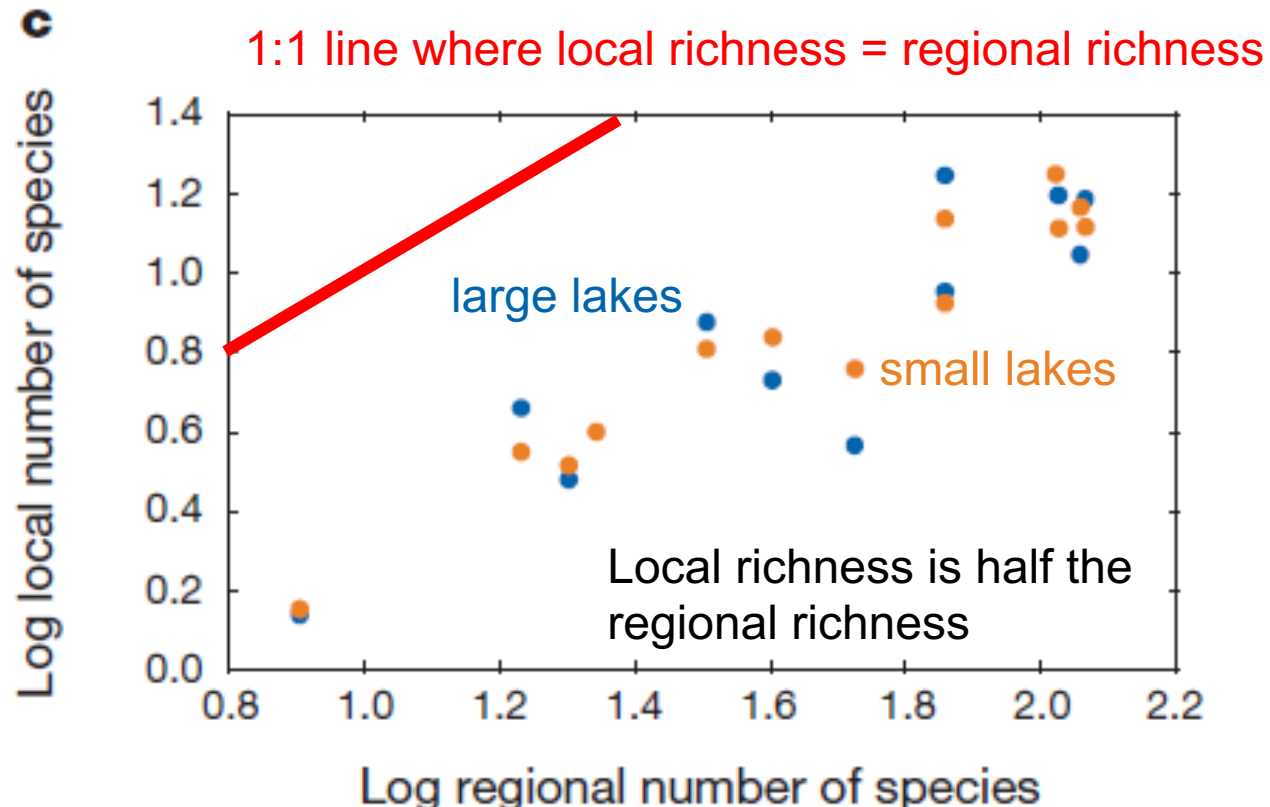
A set of communities linked by the dispersal of one or more of their constituent species

Unlike in local communities, species in a metacommunity may not actually compete due to separation in space and time



Local species richness is subset from the larger regional species pool

Lacustrine fish in North America



local richness depends on ecosystem size and connectivity to the 'metacommunity'

Connectivity by dispersal increases similarity of local pool with the regional pool

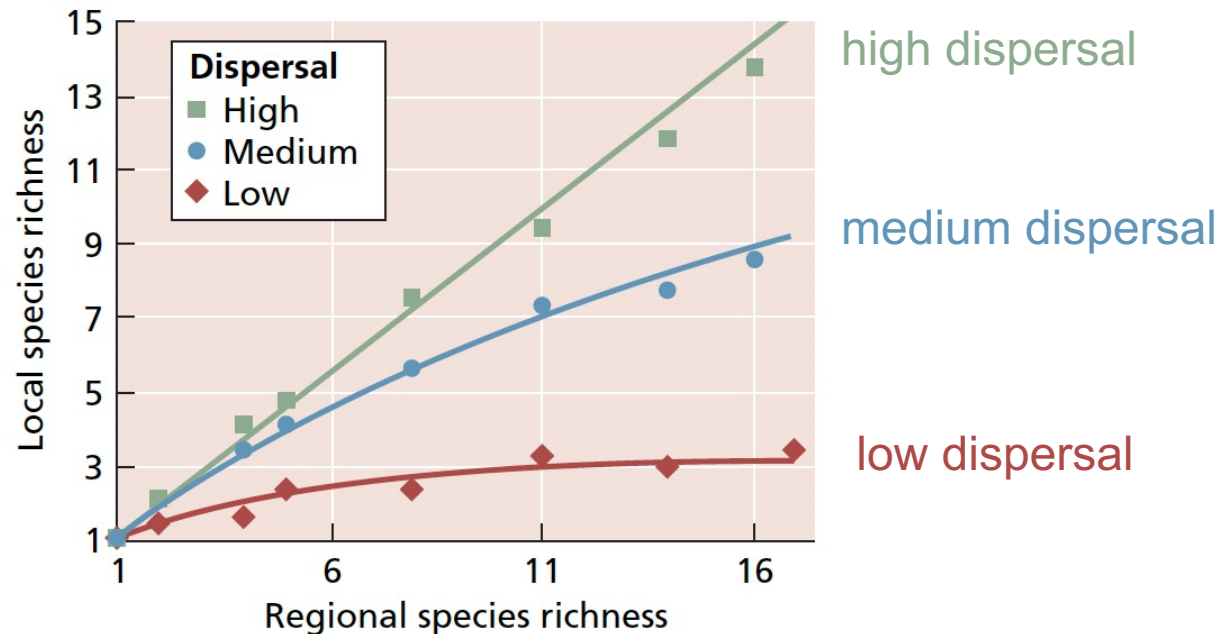


Figure 14.3 The expected relationship between local and regional species richness at different degrees of dispersal between communities in Mouquet and Loreau's metacommunity model. When dispersal between communities is relatively high, local richness is proportional to regional richness (a linear function). As dispersal decreases, the local-to-regional richness relationship becomes curvilinear and saturating due to competitive exclusion within communities. After Mouquet and Loreau (2003).

NB: the "high" dispersal case in this figure is $\alpha = 0.1$ which is still well below the value of α_{\max} in Figure 14.2.

Mouquet, N & Loreau, M (2003).
Community Patterns in Source-Sink
Metacommunities.
The American Naturalist, 162, 544-557.

2. Neutral macroecology

SCIENCE'S COMPASS



• REVIEW

REVIEW: ECOLOGY

Neutral Macroecology

Graham Bell

The central themes of community ecology—distribution, abundance, and diversity—display strongly marked and very general patterns. These include the log-normal distribution of abundance, the relation between range and abundance, the species-area law, and the turnover of species composition. Each pattern is the subject of a large literature that interprets it in terms of ecological processes, typically involving the sorting of differently specialized species onto heterogeneous landscapes. All of these patterns can be shown to arise, however, from neutral community models in which all individuals have identical properties, as the consequence of local dispersal alone. This implies, at the least, that functional interpretations of these patterns must be reevaluated. More fundamentally, neutral community models provide a general theory for biodiversity and conservation biology capable of predicting the fundamental processes and patterns of community ecology.



Neutral models

- Assume all species are equivalent
- Stochastic replacement of dead individuals with births or immigration

Bell G. (2001) Neutral Macroecology. *Science* **293**, 2413-2418.

Hubbell SP. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton.

Neutral theory can provide compelling biological patterns

Simple model requires only

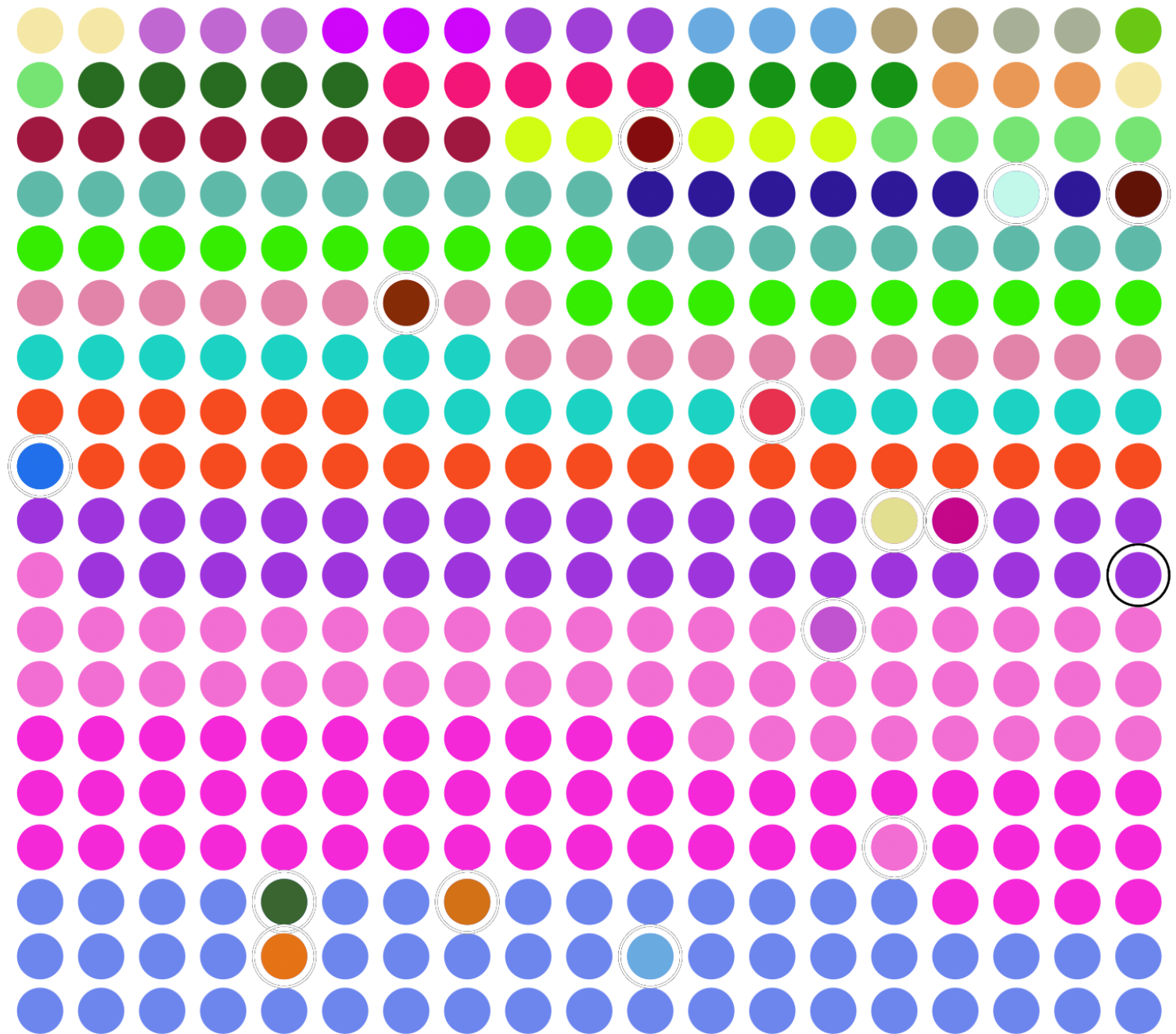
b birth,

d death,

m immigration,

K local community size and

N size of external regional pool (or metacommunity)

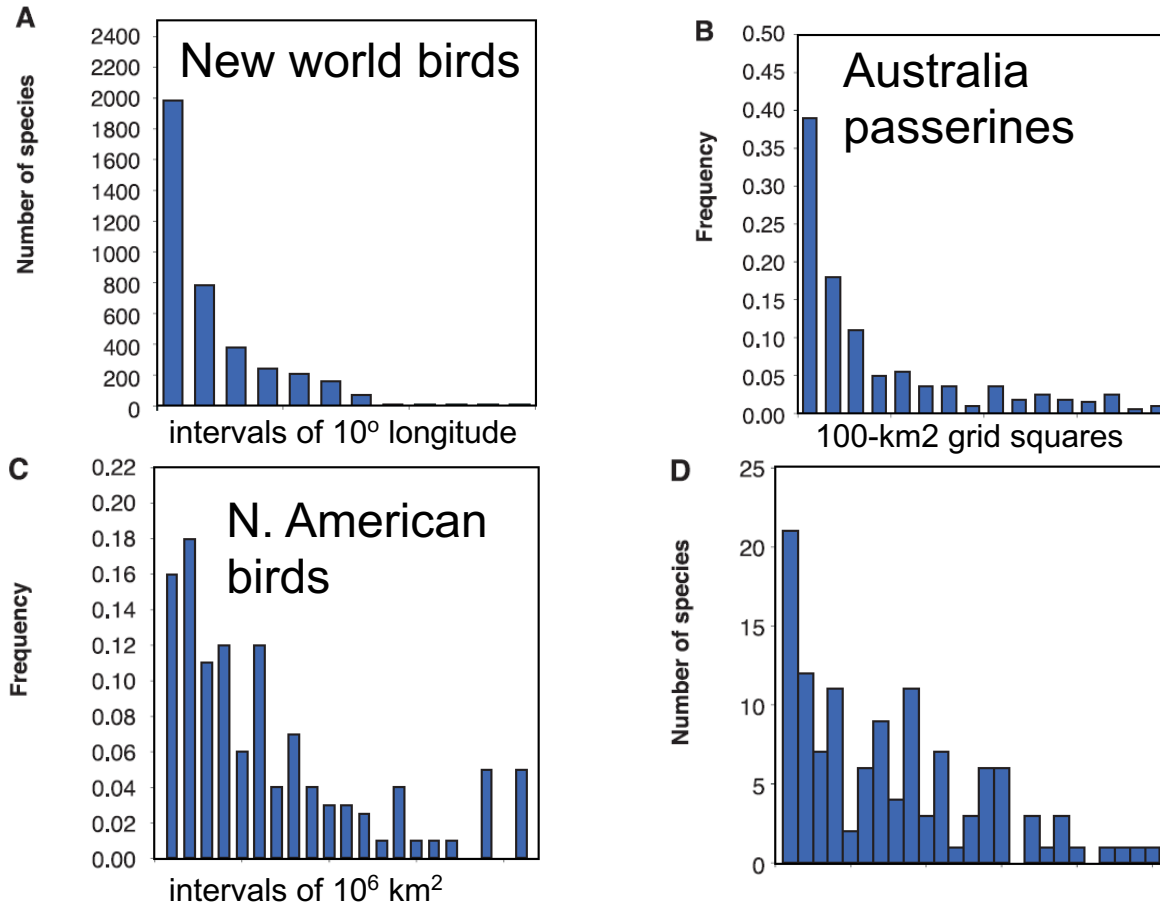


Bell neutrality

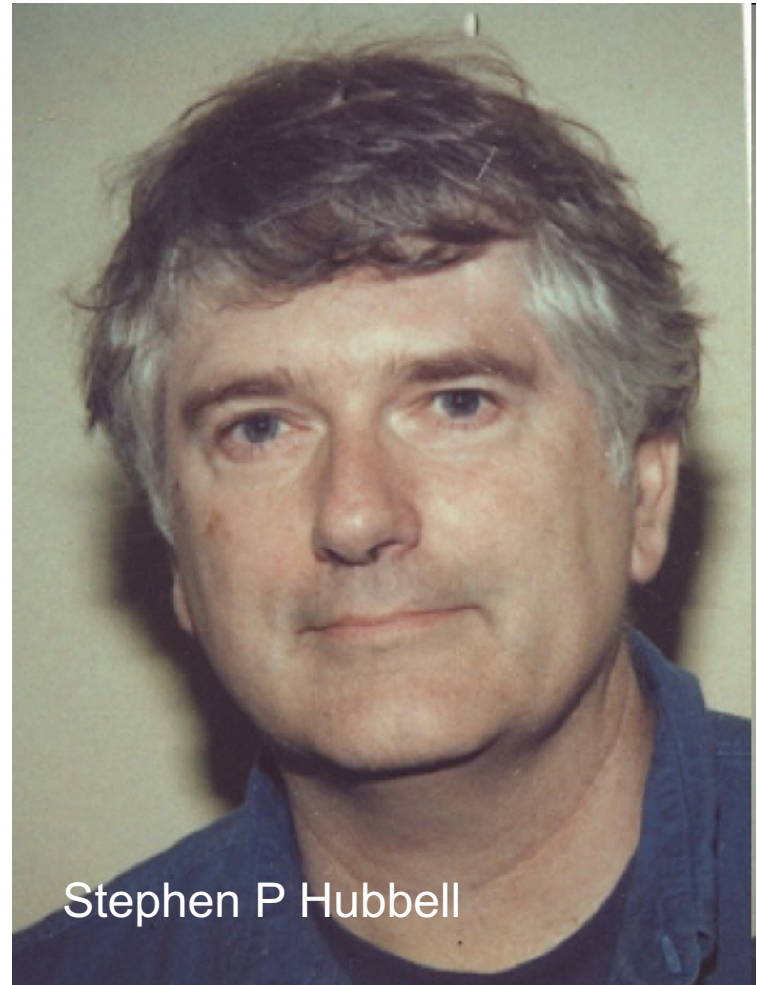
Inoculate local pool (grid) with species randomly drawn from external 'regional' pool

1. Add single individual with probability m ,
2. Residents give birth with probability b
3. and dies with probability d ,
4. If # individuals $> K$ then kill excess at random

Neutrality generates plausible geographic range size distributions



3. Unified Neutral Theory of Biodiversity (UNTB)



Stephen P Hubbell

How can there be 300 species of tree in 50 ha?
Are there 300 niches?

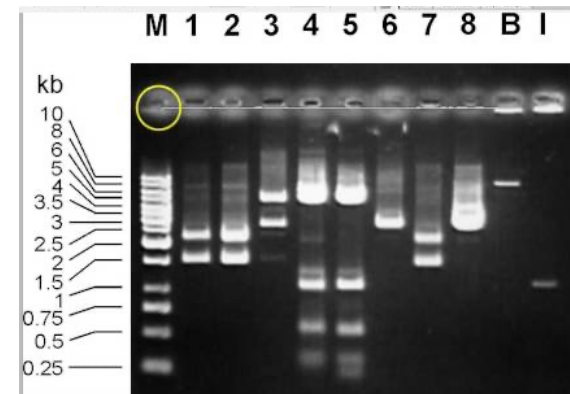


Barro Colorado Island in Lago Gatún, Panama Canal

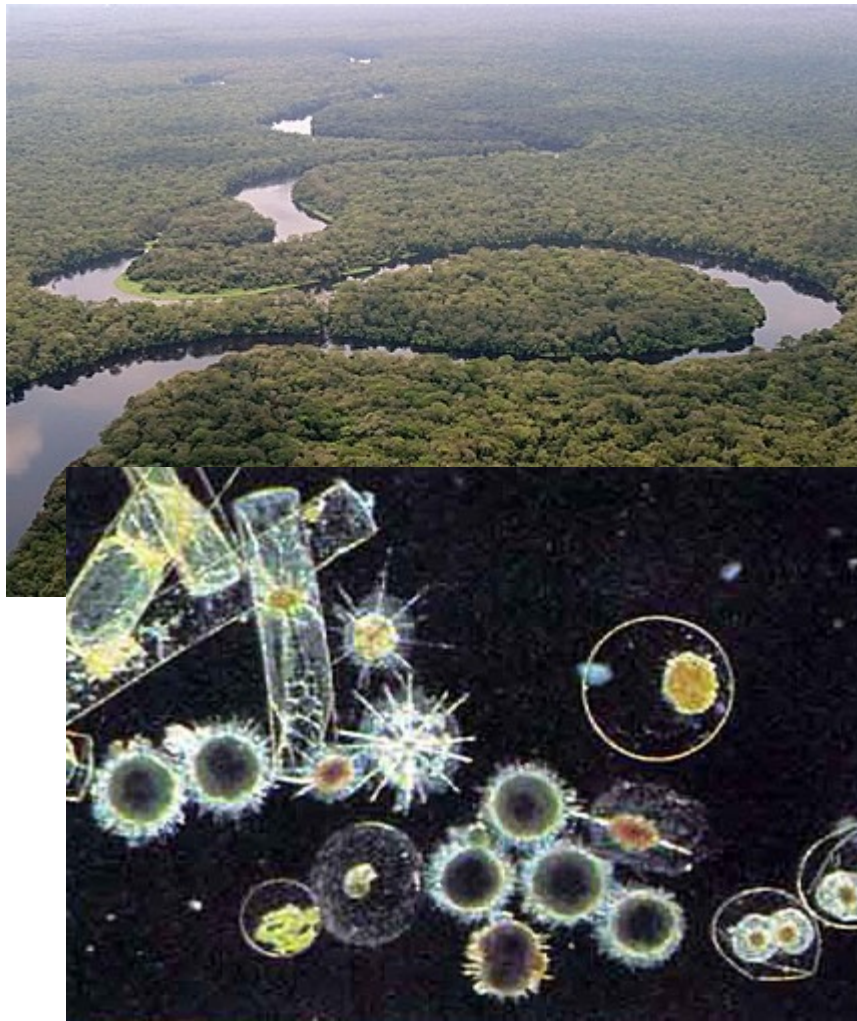
Hubbell SP. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton.

Instead, what if trees were functionally equivalent?

- What if interactions were nearly neutral w.r.t. difference between species?
- Draws upon population genetics theory which revealed that allele polymorphism was too high to be maintained by selection, concluding most alleles must be selectively neutral
 - Mutations that arise are neutral in effect
 - Frequencies of mutations in the population fluctuate at random



NB: horizontal single trophic-level ecology – Local community shares a single energy source, i.e. primary producers



Two fundamental assumptions of Neutral theory

1. Saturated local community – the number of individuals is constant, hence space is limiting, if an individual dies its place is taken by another birth or immigrant.

This is called a *zero-sum game*, and consequently competition is intense but unrelated to species-specific traits that might influence a species' contribution to community saturation

Two fundamental assumptions of Neutral theory

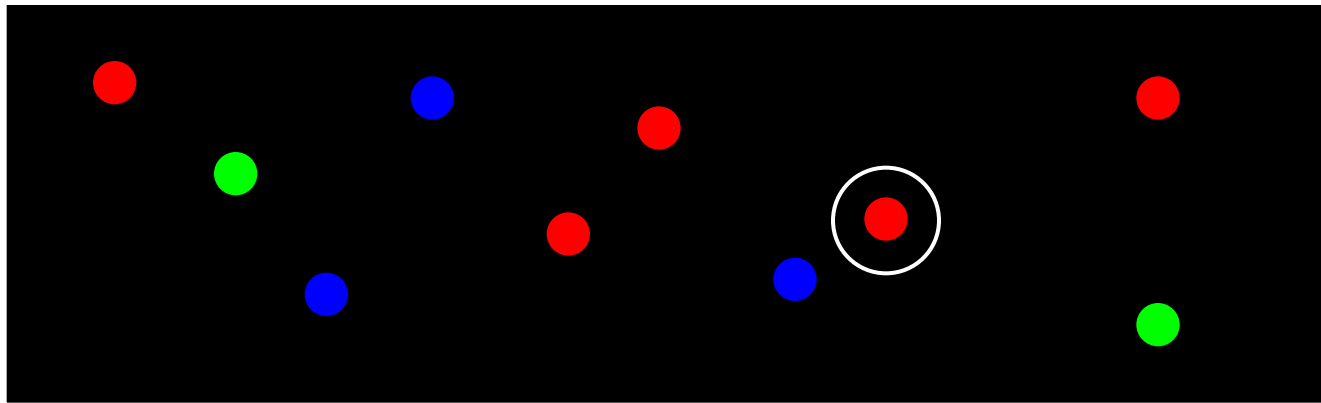
2. Ecological equivalence – all individuals belonging to all species are equivalent. A dead individual is randomly drawn from the individuals present and probability of being selected depends on relative abundance (and or immigration from regional pool).

Individuals have no traits associated with species identity that influence reproductive success, longevity, movements or likelihood of speciation.

Ecological interactions (competition or cooperation) are allowed as long as all individuals obey all rules

Ecological Equivalence: All individuals of all species are identical

Three species, $S=3$

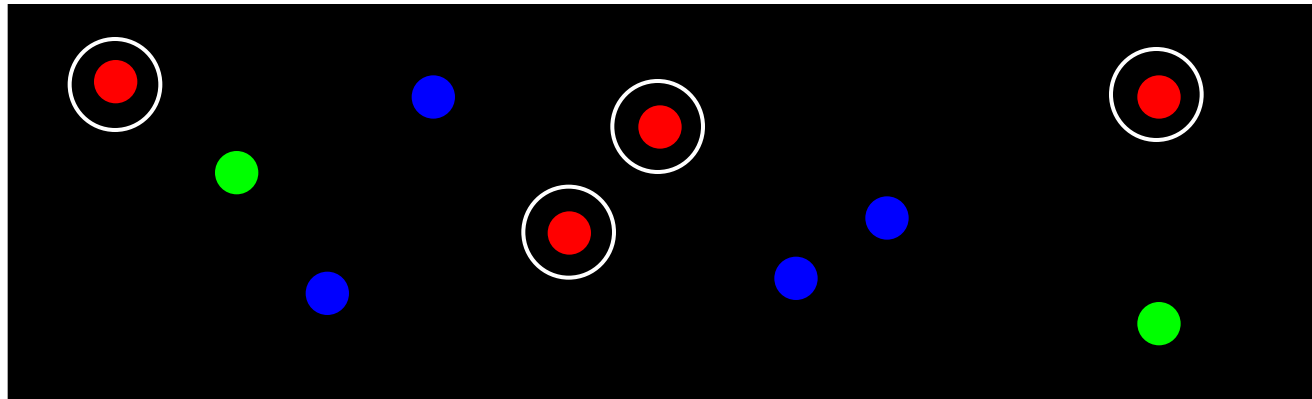


#spA=4
#spB=4
#spC=2

at each iteration:

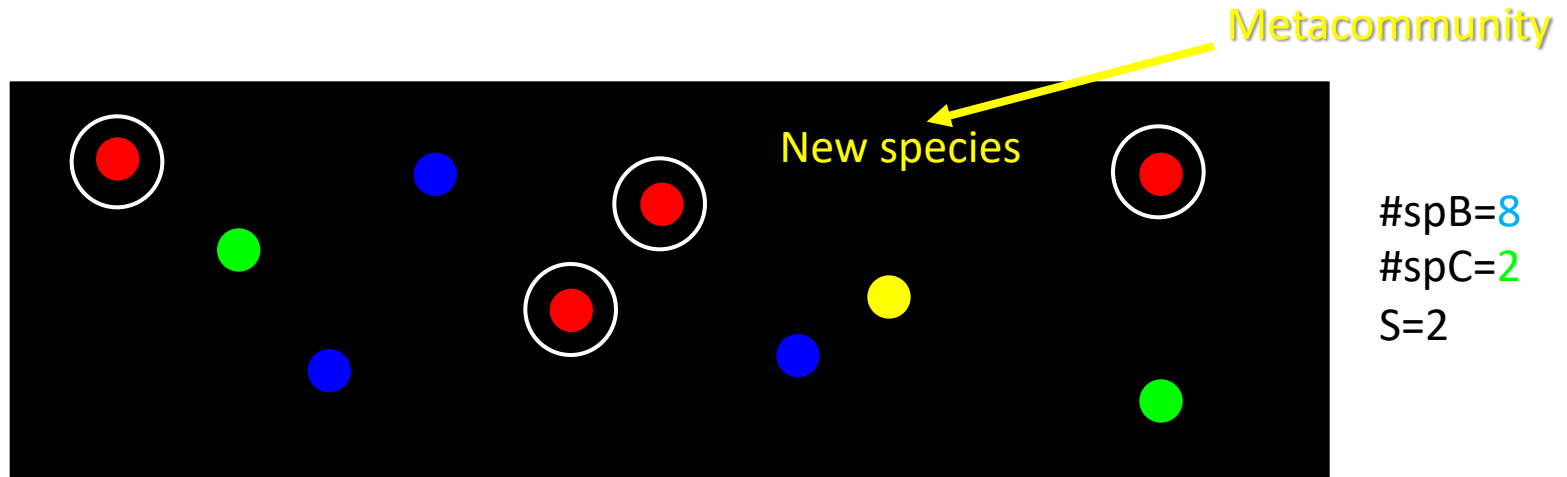
- one individual is picked up at random and replaced by a new individual.
- It could be the same species or a different one.
- This process makes species relative abundances vary through time

At local scale, rarer species go extinct over time and *dominance* increases as



As population size of a species declines stochastically, extinction risk increases

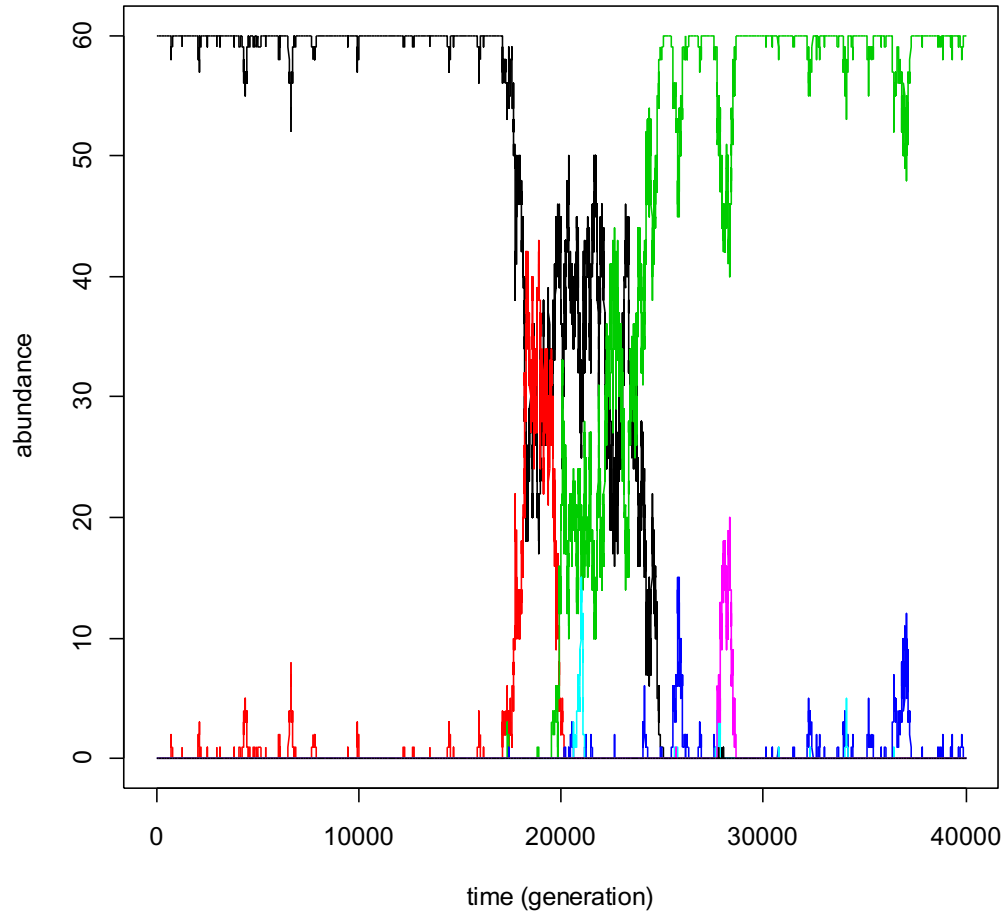
Richness maintained by immigration from the metacommunity or regional species pool



- Species diversity in the local community is maintained by immigration from a larger metacommunity
- Regionally abundant species also tend to be locally abundant

➡ Ecological drift describes how species composition of neutral assemblages varies through time.

A neutral community over time



Ecological drift in action

```
install.packages("untb")
```

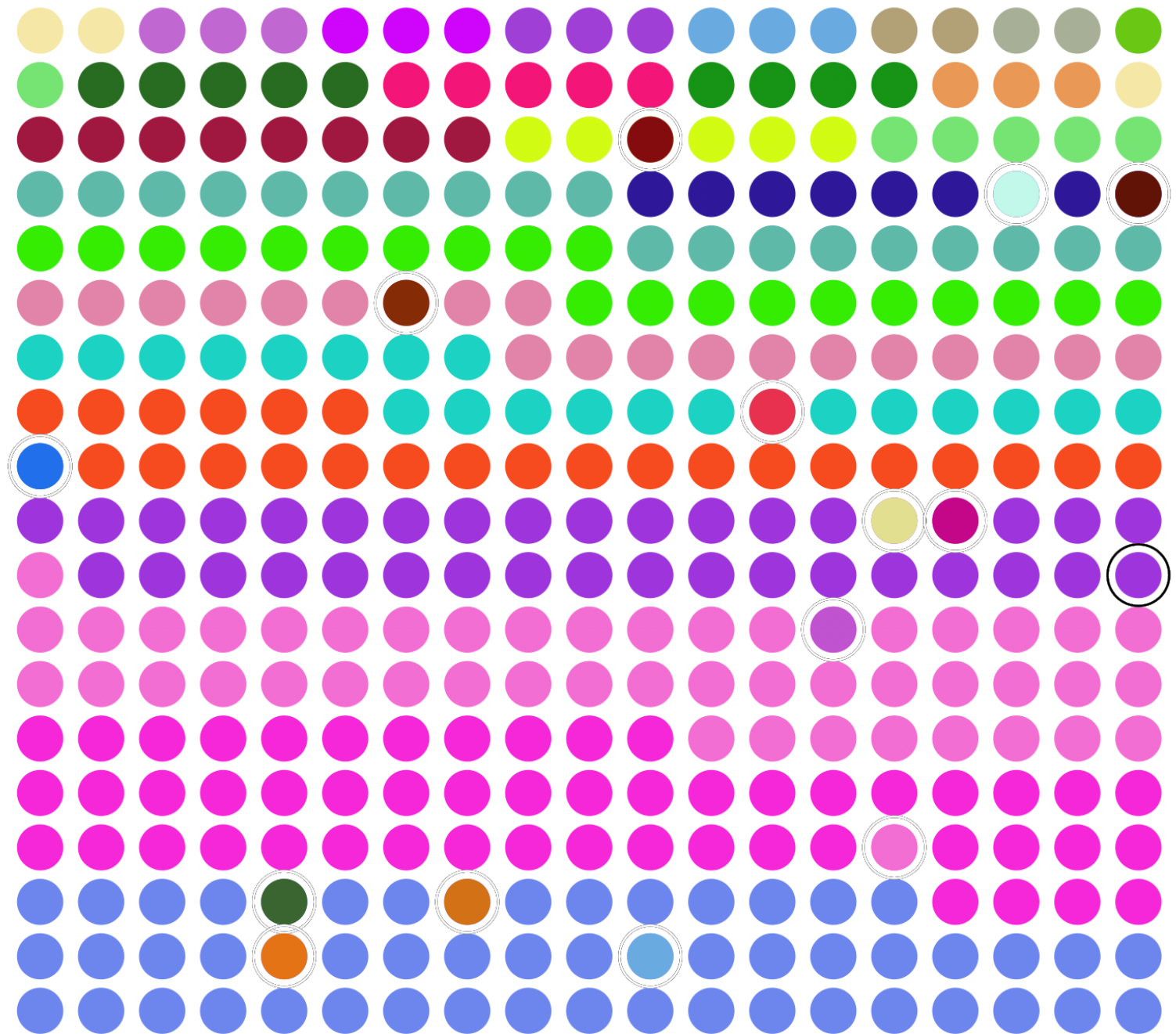
```
library(untb)
```

```
data(butterflies)
```

```
# flashing circle to show impending death & replacement
```

```
dev.new()
```

```
display.untb( start=butterflies,  
  prob=0.8, #probability of mutation  
  gens=1e1,  
  delay=0.001,  
  cex=3,  
  flash=TRUE)
```



The fundamental biodiversity number θ (θ)

Fundamental biodiversity number $\theta = 2Jv$, where

J is the community size (#individuals),
 v is the speciation rate

For a given community size J ,

High speciation rate $\theta \Rightarrow$ evenness and many rare species

Low speciation rate $\theta \Rightarrow$ high dominance and few rare species

Generations

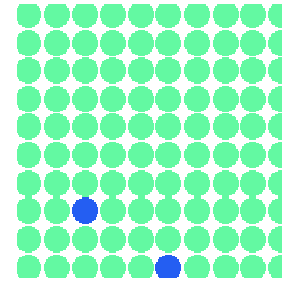
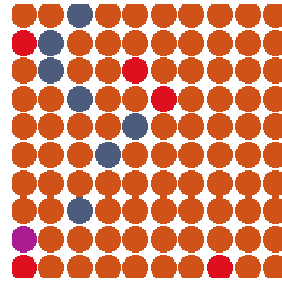
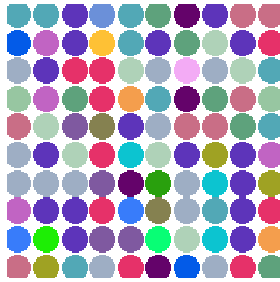
t=10

t=50

t=100

$\theta=0$

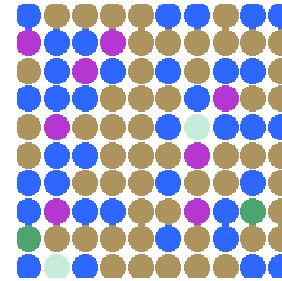
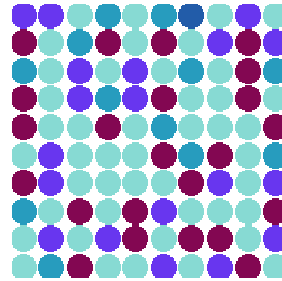
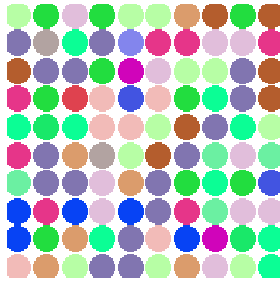
$\theta=0$



Small community &
low speciation rate θ
leads to high dominance

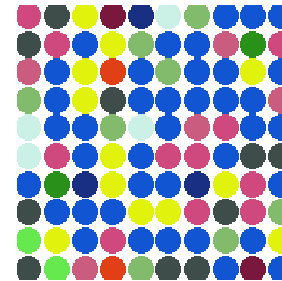
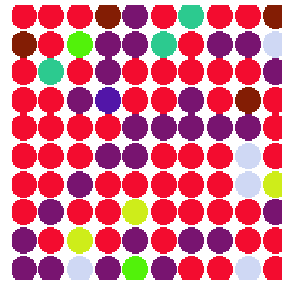
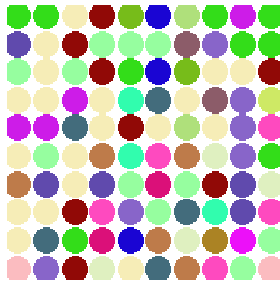
$\theta=0.1$

$\theta=0.1$



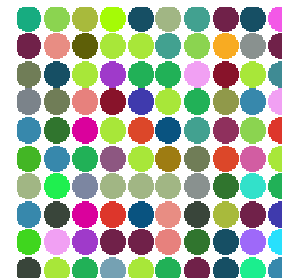
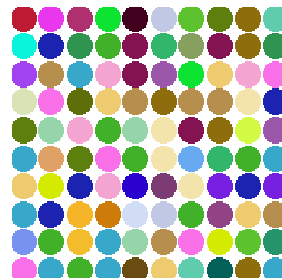
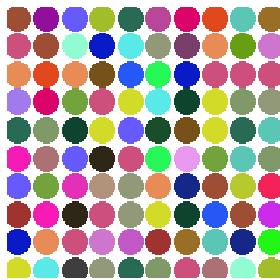
$\theta=1$

$\theta=1$

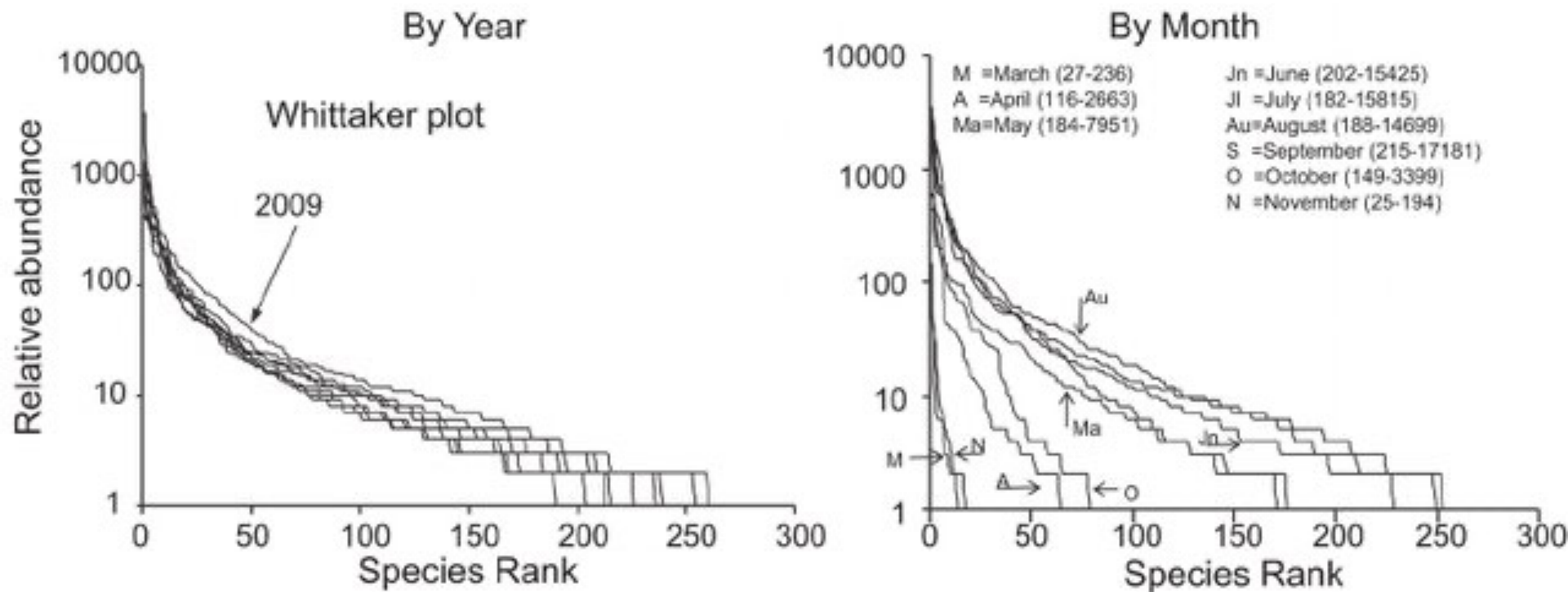


$\theta=10$

$\theta=10$

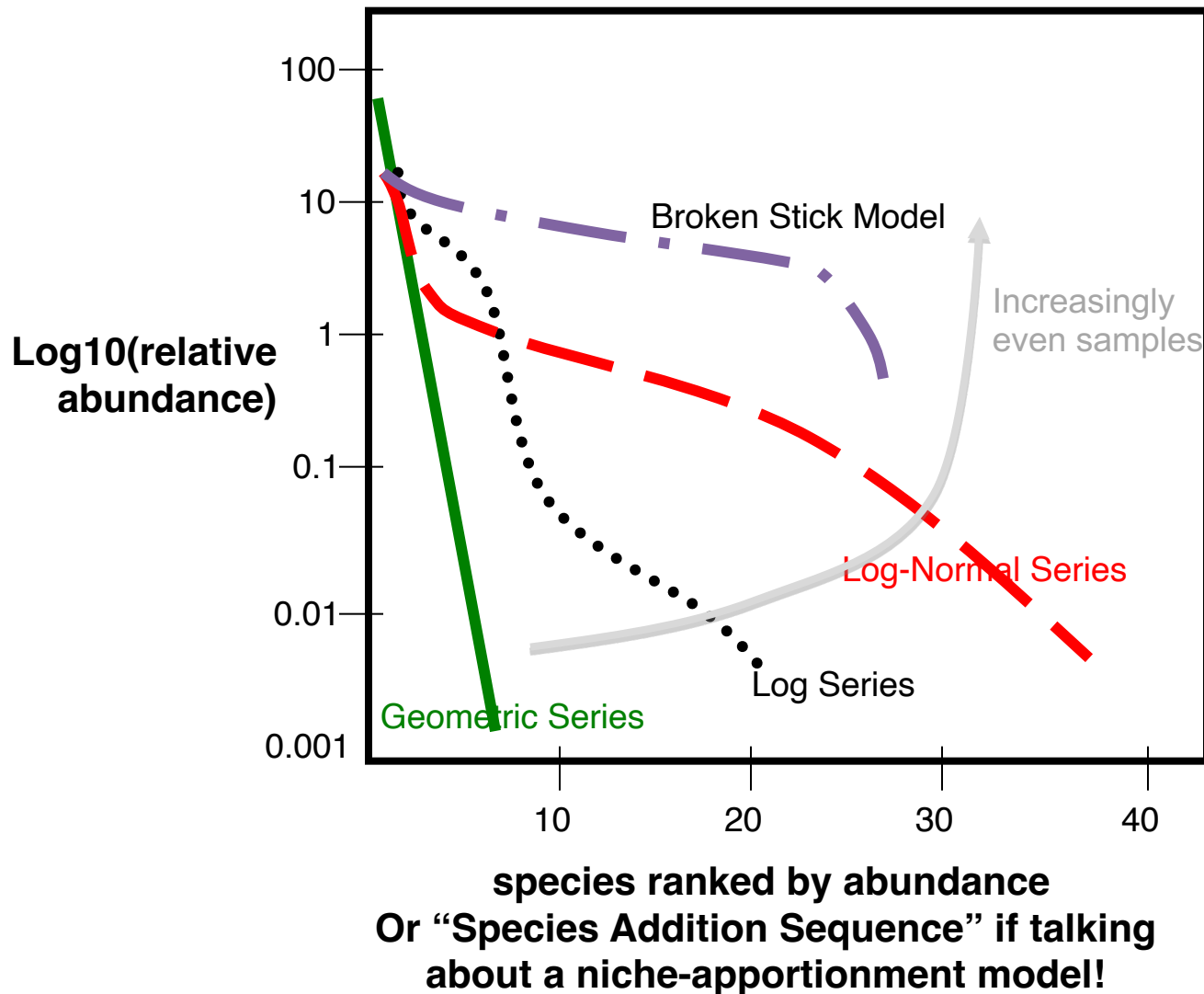


Larger community &
high speciation rate θ
leads to low dominance

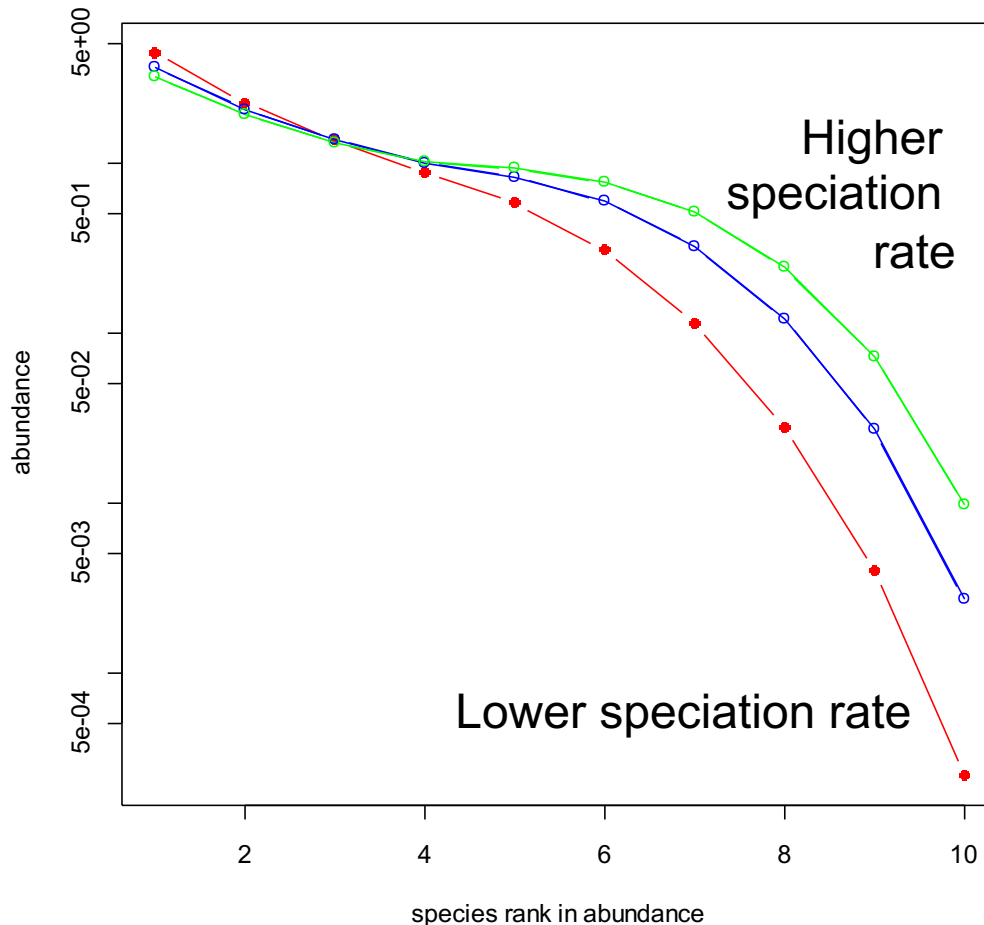


Downer RA and Ebert TA. (2014) Macrolepidoptera biodiversity in Wooster, Ohio from 2001 through 2009. *Zookeys*, 79.

A Whittaker plot of species ranked by relative abundance



Larger speciation rate θ leads to low dominance (flat curves)



Size of ecosystem – $J = 10$ spp

$\Theta = 7$ flatter curve, less dominance

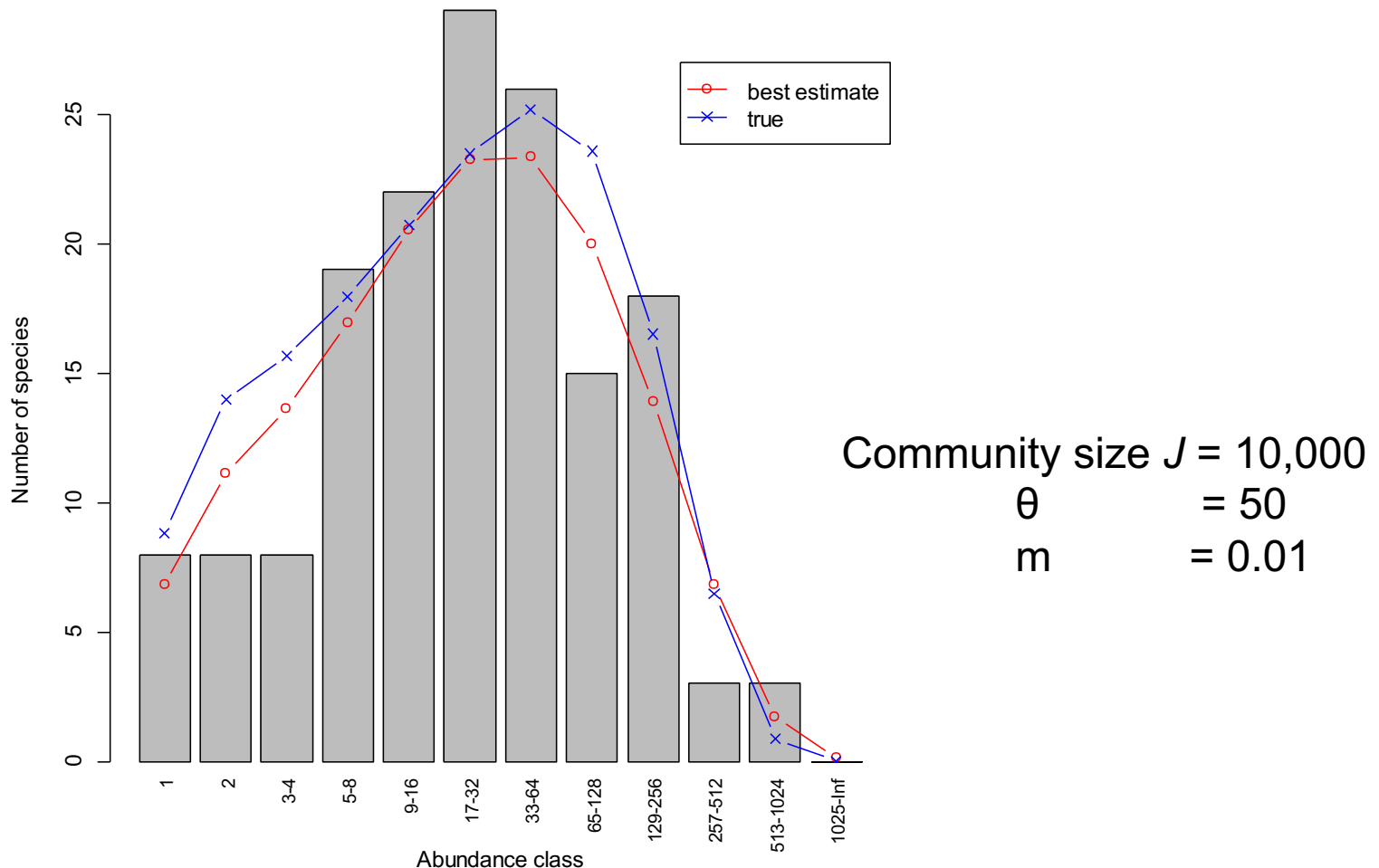
$\Theta = 5$

$\Theta = 3$

A niche argument is not needed
to explain relative species
abundance plots

Simply varying community size j and
speciation rate ν ($\theta = 2J\nu$) is enough

Neutrality can account for large numbers of singletons



e.g., Volkov I, Banavar JR, Hubbell SP and Maritan A. (2003) Neutral theory and relative species abundance in ecology. *Nature* **424**, 1035-1037.

Self-organized similarity, the evolutionary emergence of groups of similar species

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Edited by Stephen R. Carpenter, University of Wisconsin, Madison, WI, and approved February 21, 2006 (received for review September 16, 2005)

Ecologists have long been puzzled by the fact that there are so many similar species in nature. Here we show that self-organized clusters of look-a-likes may emerge spontaneously from coevolution of competitors. The explanation is that there are two alternative ways to survive together: being sufficiently different or being sufficiently similar. Using a model based on classical competition theory, we demonstrate a tendency for evolutionary emergence of regularly spaced lumps of similar species along a niche axis. Indeed, such lumpy patterns are commonly observed in size distributions of organisms ranging from algae, zooplankton, and beetles to birds and mammals, and could not be well explained by earlier theory. Our results suggest that these patterns may represent self-constructed niches emerging from competitive interactions. A corollary of our findings is that, whereas in species-poor communities sympatric speciation and invasion of open niches is possible, species-saturated communities may be characterized by convergent evolution and invasion by look-a-likes.

biodiversity | coexistence | competition | evolution | niche construction

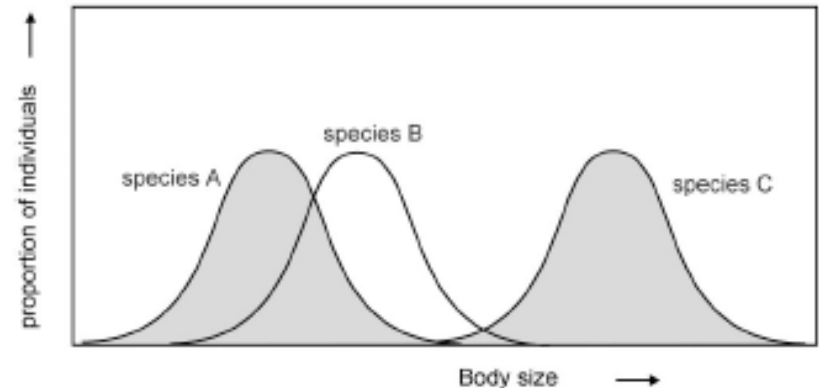


Fig. 1. To study competition, we place species randomly along a hypothetical niche axis. To facilitate an intuitive interpretation, one may think of the niche axis as a gradient that is related to the size of organisms. If we assume that individuals of the same size compete strongest, niche overlap and resulting competition coefficients can be computed (45) for sets of species of given size distributions (see *Methods*).

Classic Lotka-Volterra model

$\alpha_{i,j}$ is the competition coefficient of species j on i

N_j is the abundance of species j

$$\frac{dN_i}{dt} = rN_i \left(\frac{K - \sum_j \alpha_{i,j} N_j}{K} \right),$$










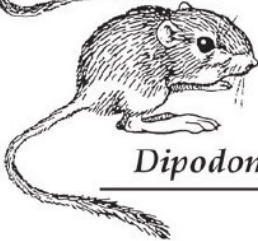
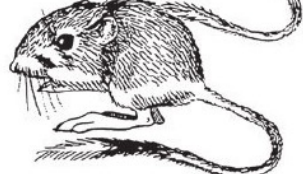
Community level patterns

EG Differences among species in communities



■ Great Basin Desert
■ Sonoran Desert

Body weight (g)

Great Basin Desert		Sonoran Desert	
<i>Perognathus longimembris</i>	7.1	<i>Perognathus flavus</i>	
	7.2		
	11.4	<i>Reithrodontomys megalotis</i>	
<i>Microdipodops pallidus</i>			
	12.5	<i>Perognathus penicillatus</i>	
<i>Peromyscus maniculatus</i>	17.1		
	18.1	<i>Peromyscus maniculatus</i>	
	24.3		
<i>Dipodomys merriami</i>	37.6	<i>Dipodomys merriami</i>	
	45.3		
	101		
<i>Dipodomys deserti</i>	102	<i>Dipodomys spectabilis</i>	

→ the law of limiting similarity

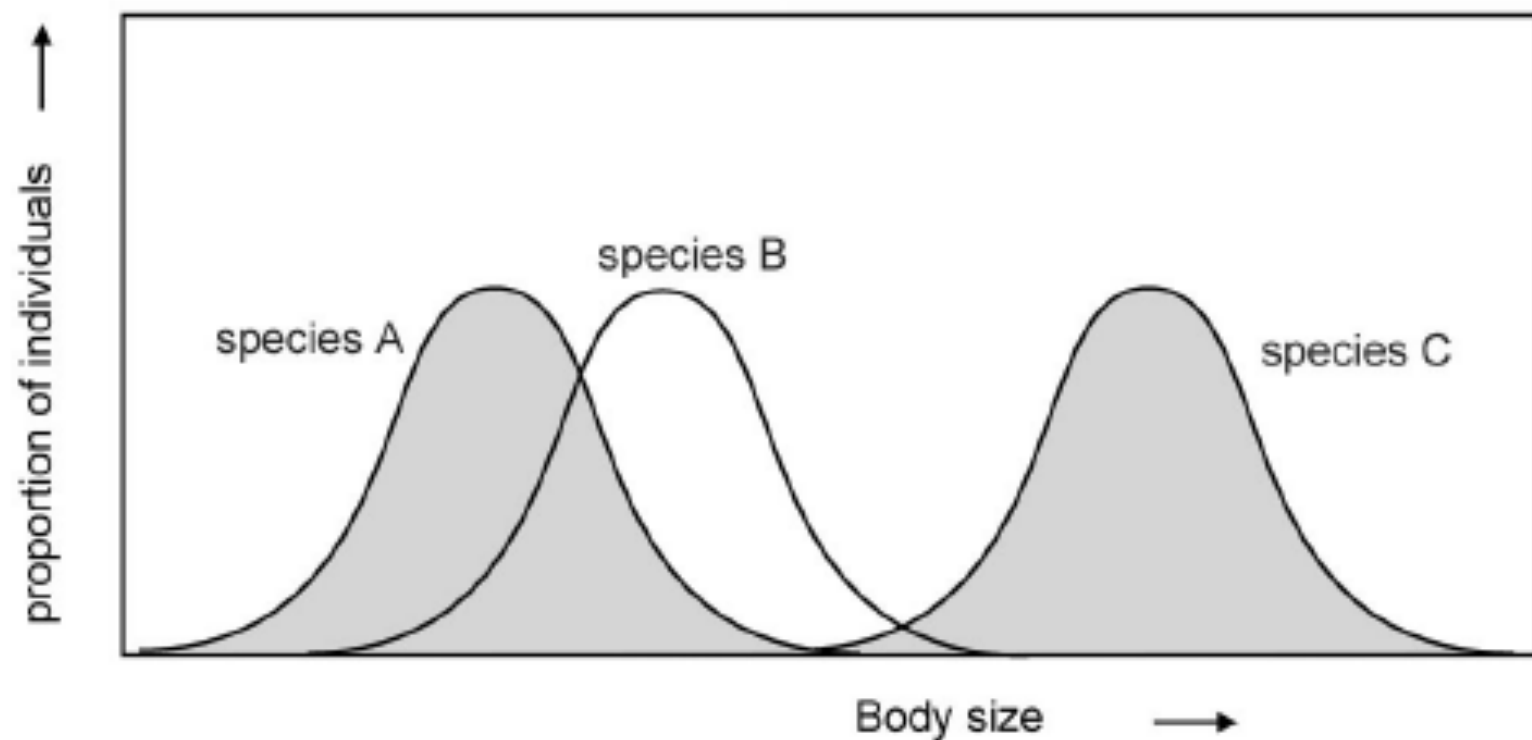
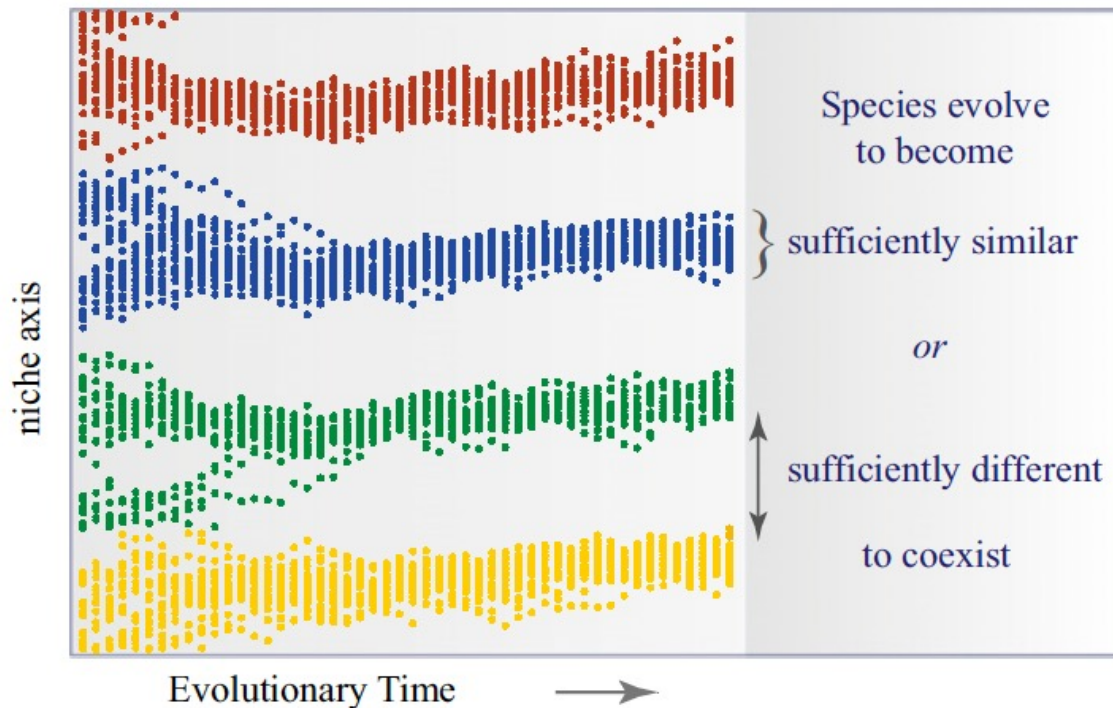


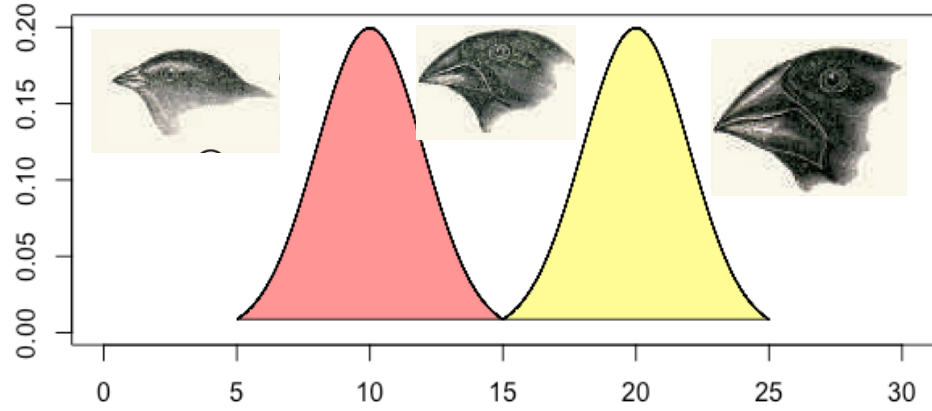
Fig. 1. To study competition, we place species randomly along a hypothetical niche axis. To facilitate an intuitive interpretation, one may think of the niche axis as a gradient that is related to the size of organisms. If we assume that individuals of the same size compete strongest, niche overlap and resulting competition coefficients can be computed (45) for sets of species of given size distributions (see *Methods*).



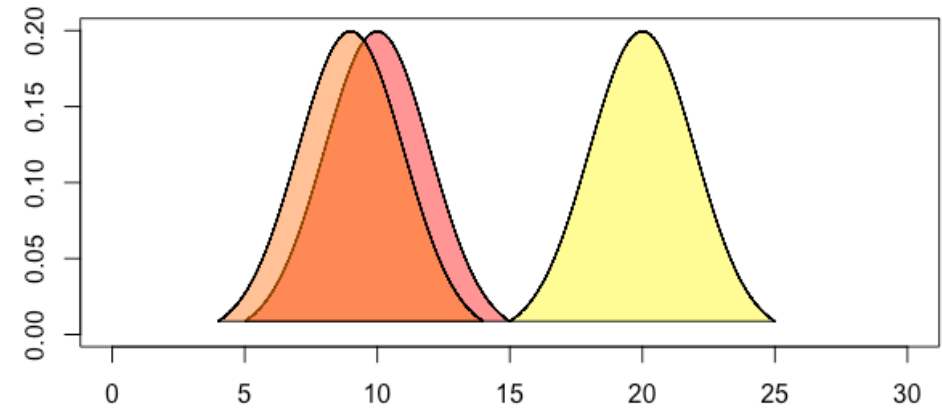
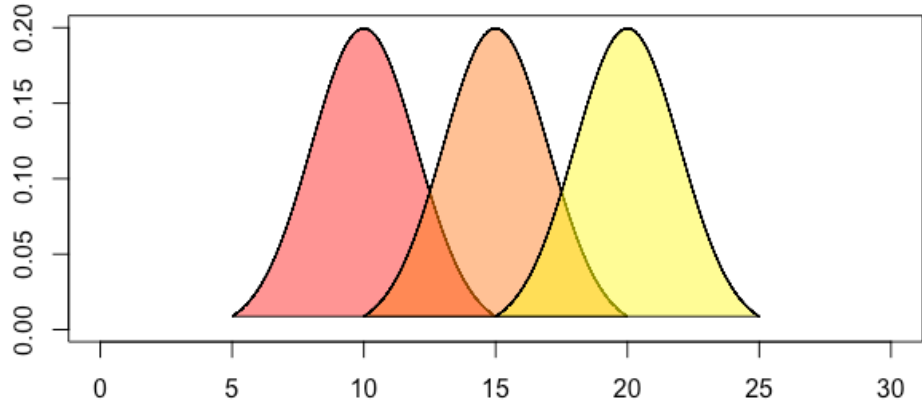
The secret of this puzzling form of coexistence is that at very high similarities the displacement rate of the weakest competitor becomes exceedingly slow.

Fig. 1. Simulation of the evolutionary adaptation of species showing the emergence of regularly spaced lumps of near-neutral coexistence. Species move away from the gaps toward the self-organized niches reflected in the lumps. The distance between the lumps corresponds to the niche separation that is theoretically predicted from the classic theory of limiting similarity. Modified with permission from ref. 4; Copyright (2006), National Academy of Sciences, USA.

Scheffer M, van Nes EH and Vergnon R. (2018) Toward a unifying theory of biodiversity. *Proc Natl Acad Sci U S A* **115**, 639-641.

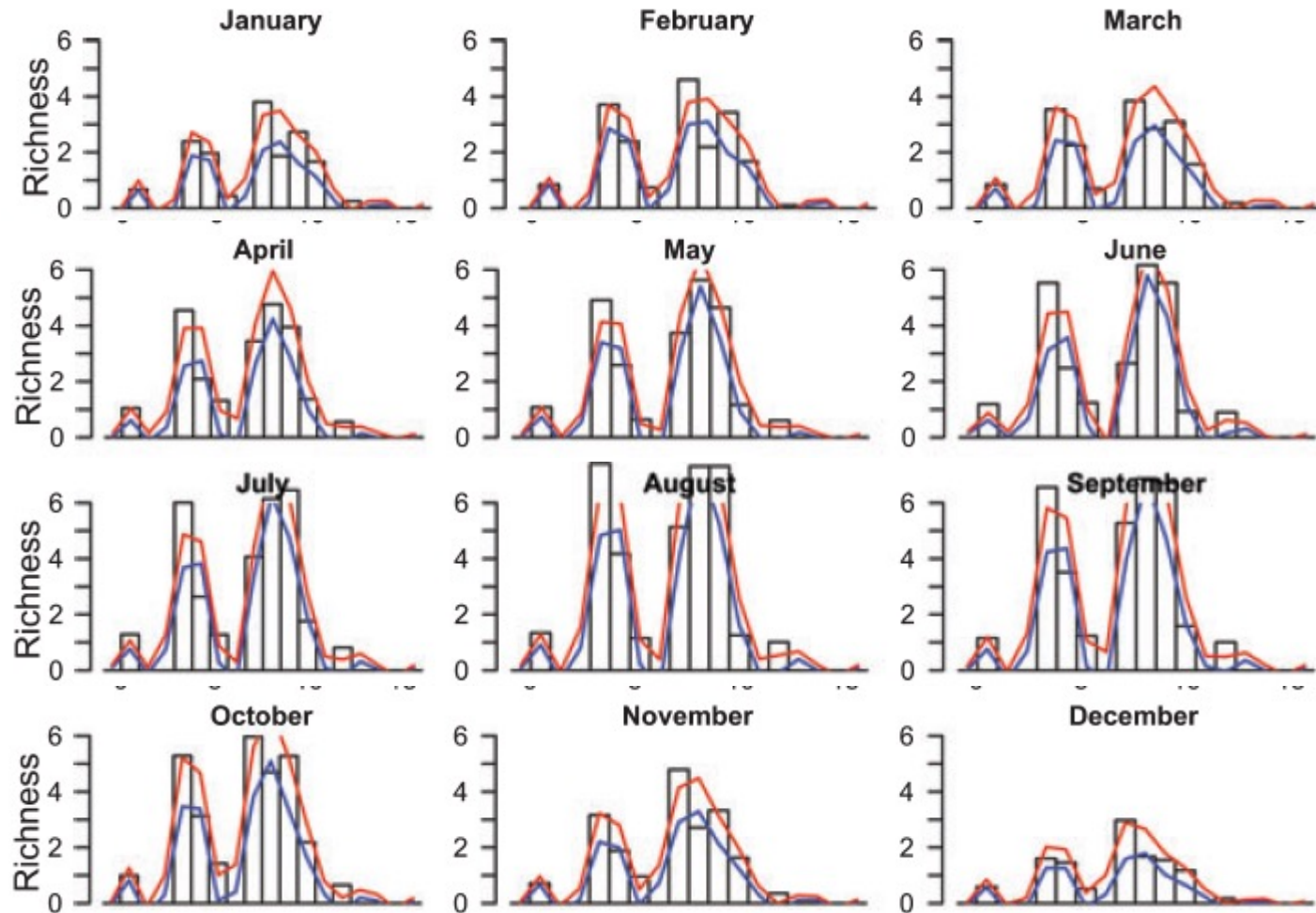


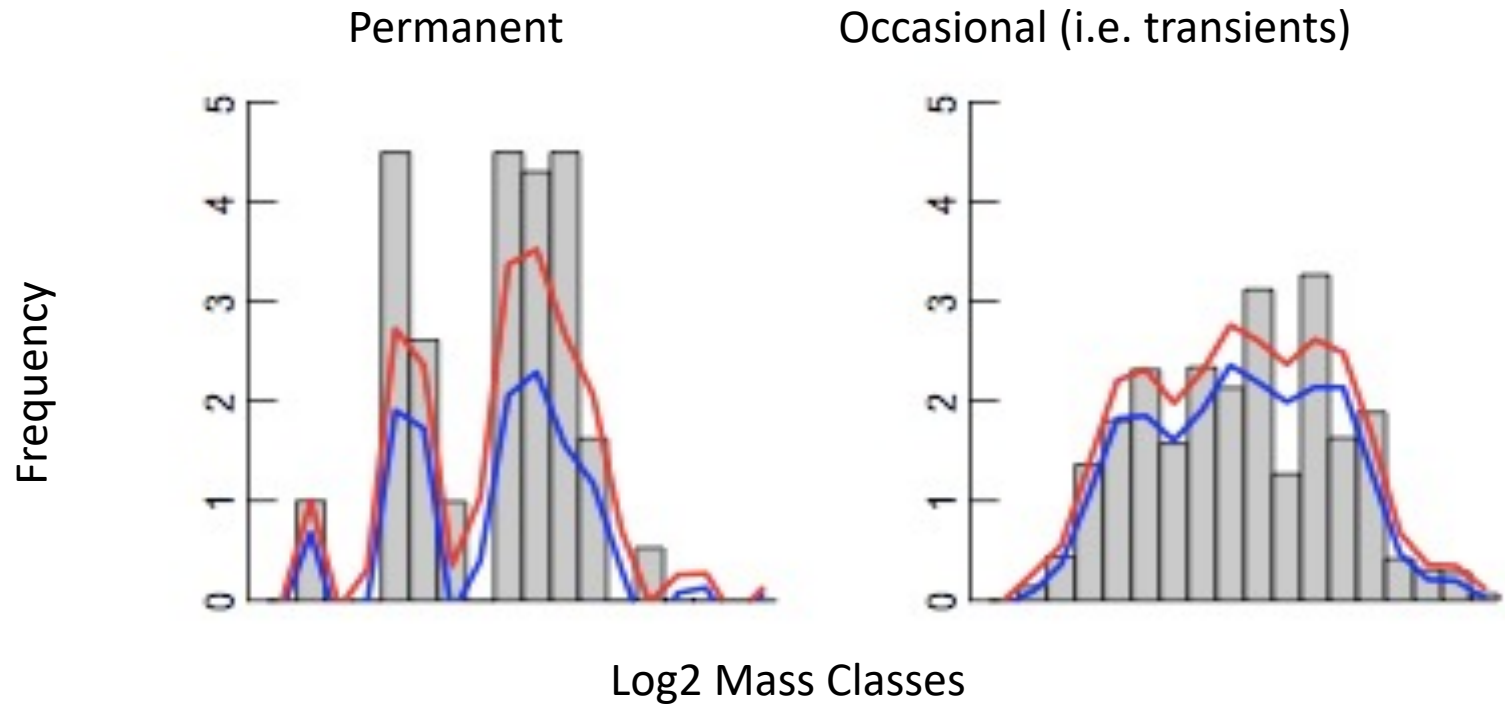
Utilization ability



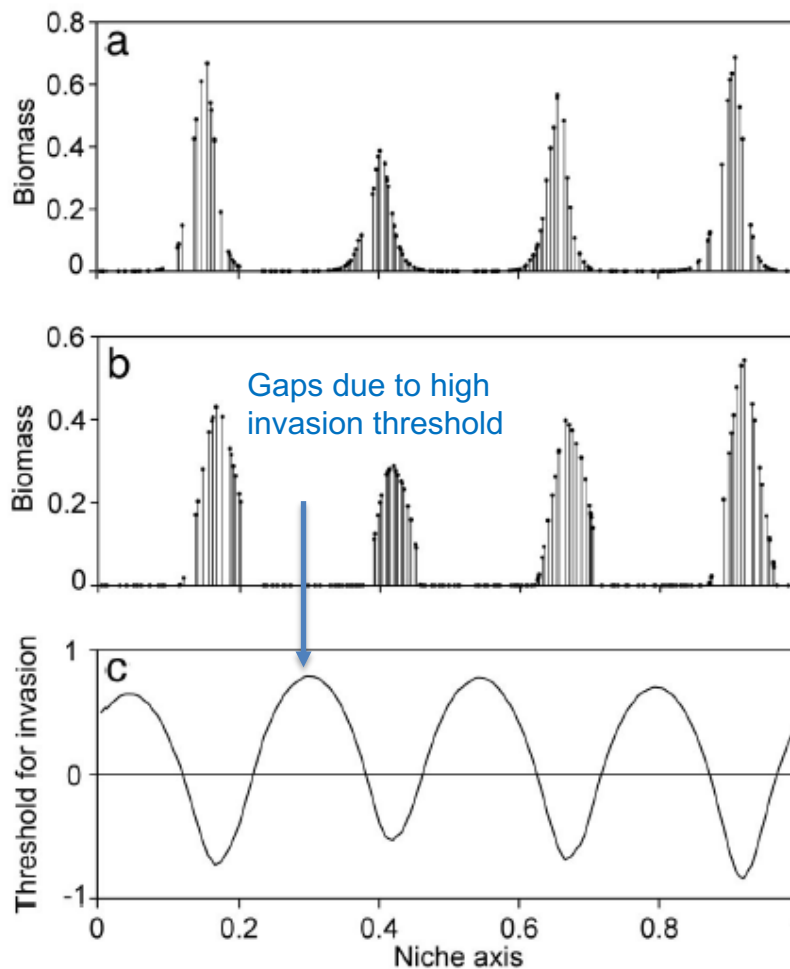
Niche axis (e.g. seed size)

Marine zooplankton richness is bi/tri-modal across the production cycle





Transient species can invade as production ramps up in summer but eventually are purged out and cannot persist due to high competition between the modes



Transient state after 1,000 gens

stable state after 5,000 gens

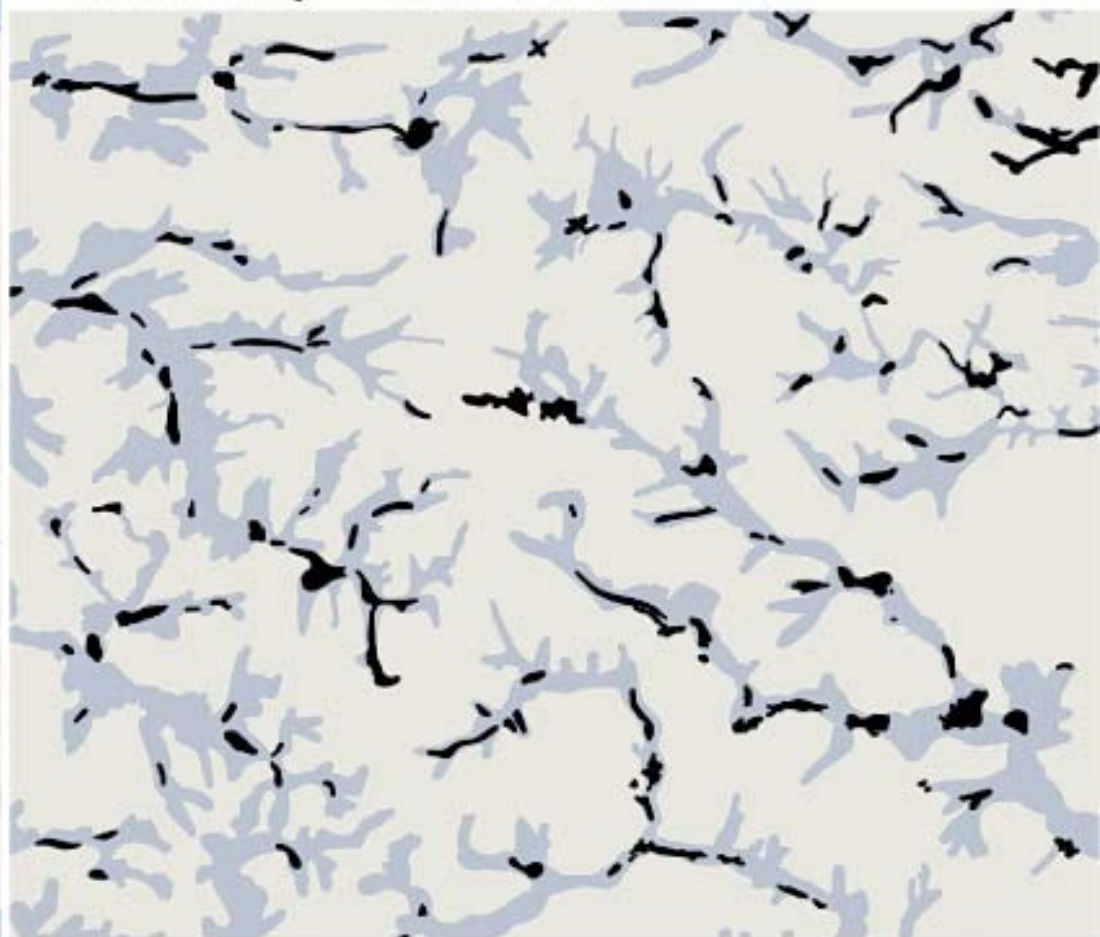
Fig. 2. Self-organized lumpy patterns in the abundance of competing species along a niche axis. (a) A transient state after a simulation run of 1,000 generation times. (b) A stable pattern of species abundance reached after 5,000 generation times in the presence of mild density-dependent losses ($g = 0.02$, $H = 0.1$, Eq. 2). (c) The competitive threshold for invasion of a new species expressed as percentage deviation of its carrying capacity (K) relative to that of the resident species is lowest in the species lumps, showing that these represent relative windows of opportunity for invasion, and attractors in the fitness landscape. Note that the relatively low predation loss at low densities allows starting invaders to enter with a competitive power (K) slightly below that of residents.

LAND OF PLENTY

Beneath the ground in Australia's arid western plateau lie hundreds of honeycombed limestone deposits, or calcretes, formed during a dry phase between 37 and 30 million years ago



● Ancient river valleys ● Groundwater calcretes



Calcretes formed under dried-up rivers in areas where underground water came close enough to the surface to evaporate. Each one is an isolated water-filled ecosystem, riddled with tiny voids and tunnels, and home to hundreds of animal species, most of which are new to science







Subterranean fauna



Stygofauna



Troglofauna

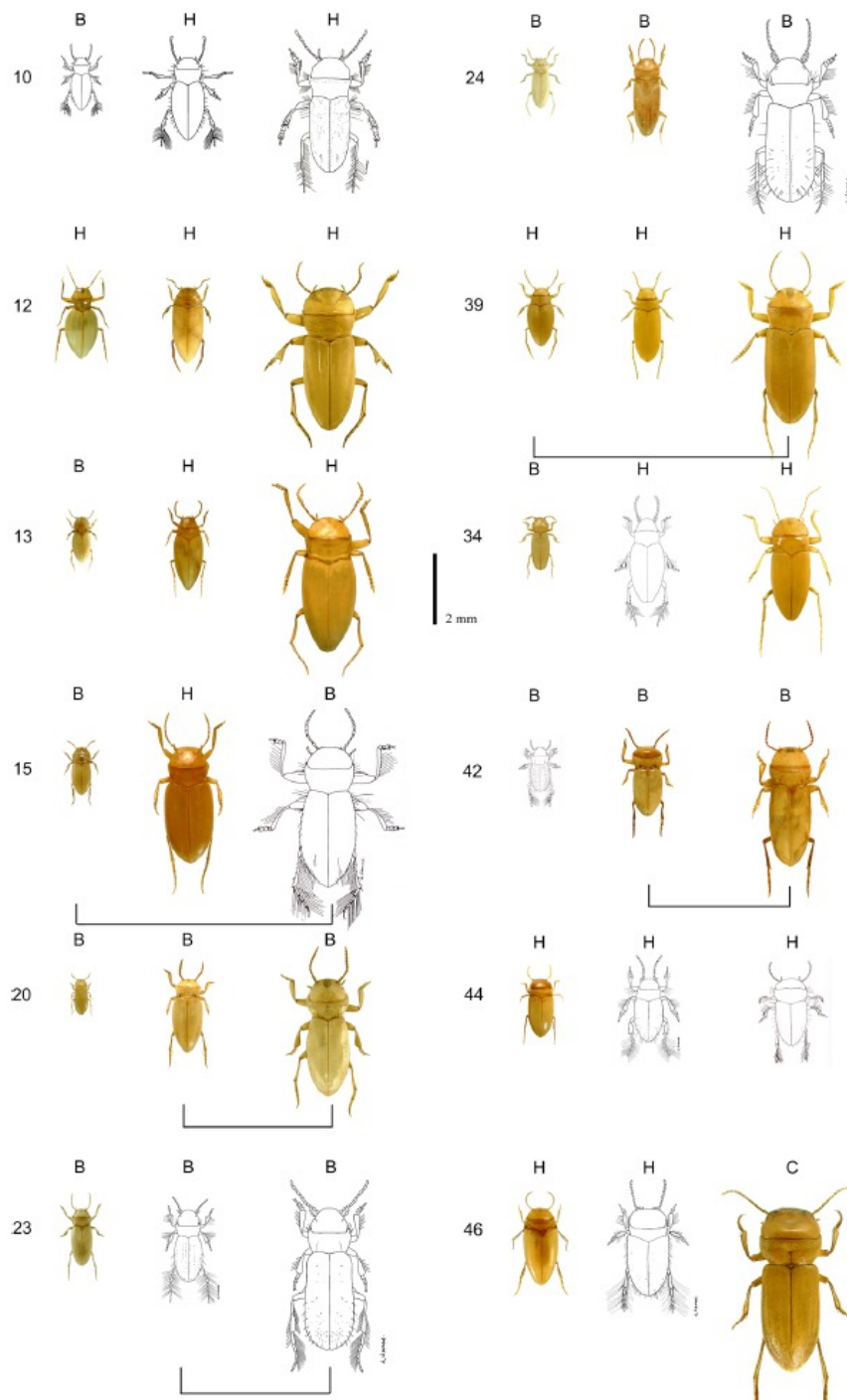


Fig 4. Communities consisting of triplets of blind diving beetle species found in different underground aquifers (numbers) that became isolated 5 million years ago when Australian climate became arid. Independently of the founder species, evolution led to a small a medium and a large species in each aquifer. H, B and C code the tribes Bidessini, Hydroporini and Copelatini; bars connect pairs of species that evolved from the same founder species (illustration courtesy of Chris Watts and Howard Hamond).

Scheffer M, Vergnon R, van Nes EH, Cuppen JGM, Peeters E, Leijss R, Nilsson AN. 2015. The Evolution of Functionally Redundant Species; Evidence from Beetles. *Plos One* **10**: 10.

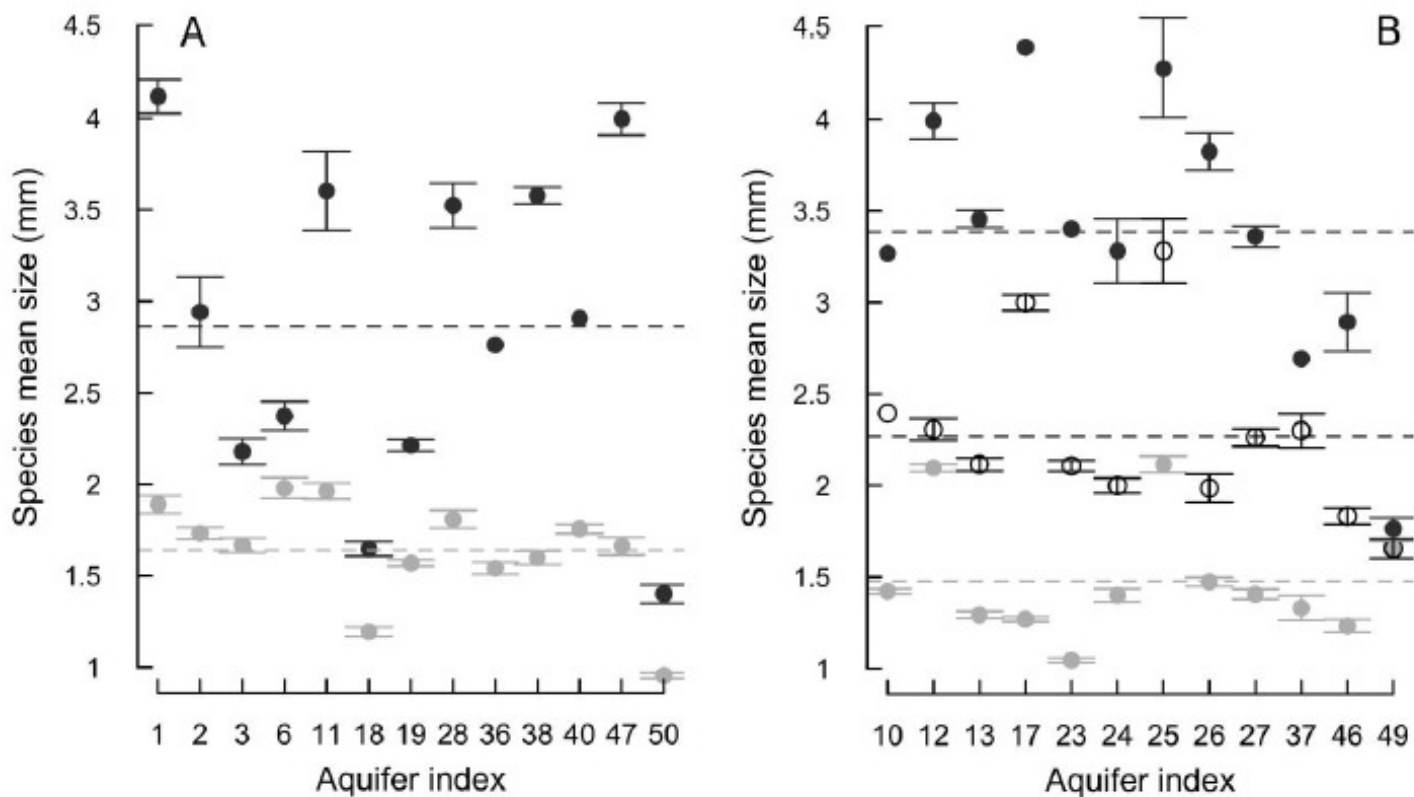
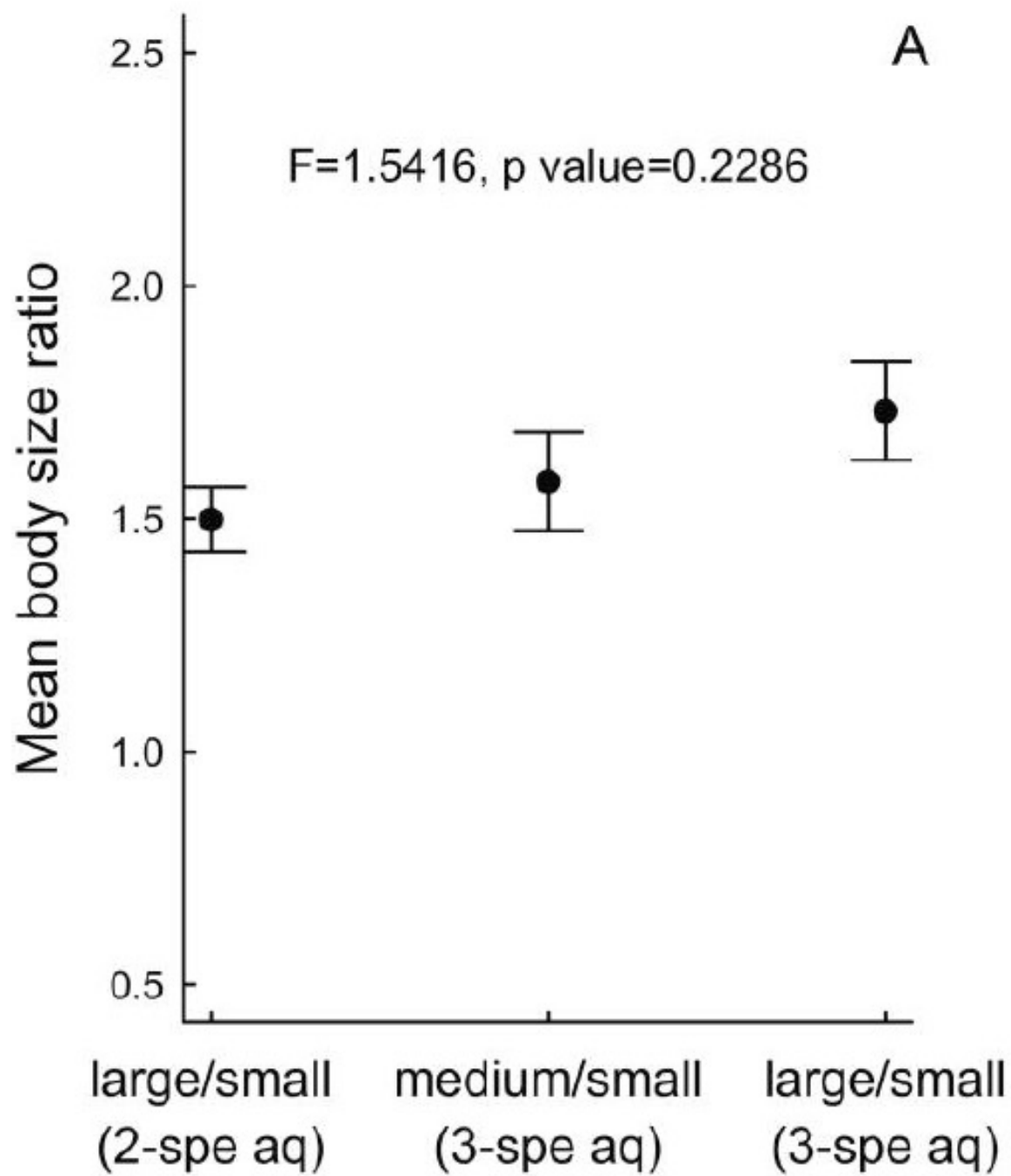


Figure 1: Mean species body sizes in millimeters with standard errors in two-species (A) and three-species (B) aquifers. Different colors correspond to different species size ranks: small (gray), medium (white), and large (black). Aquifer indexes are as in Watts and Humphreys (2009).



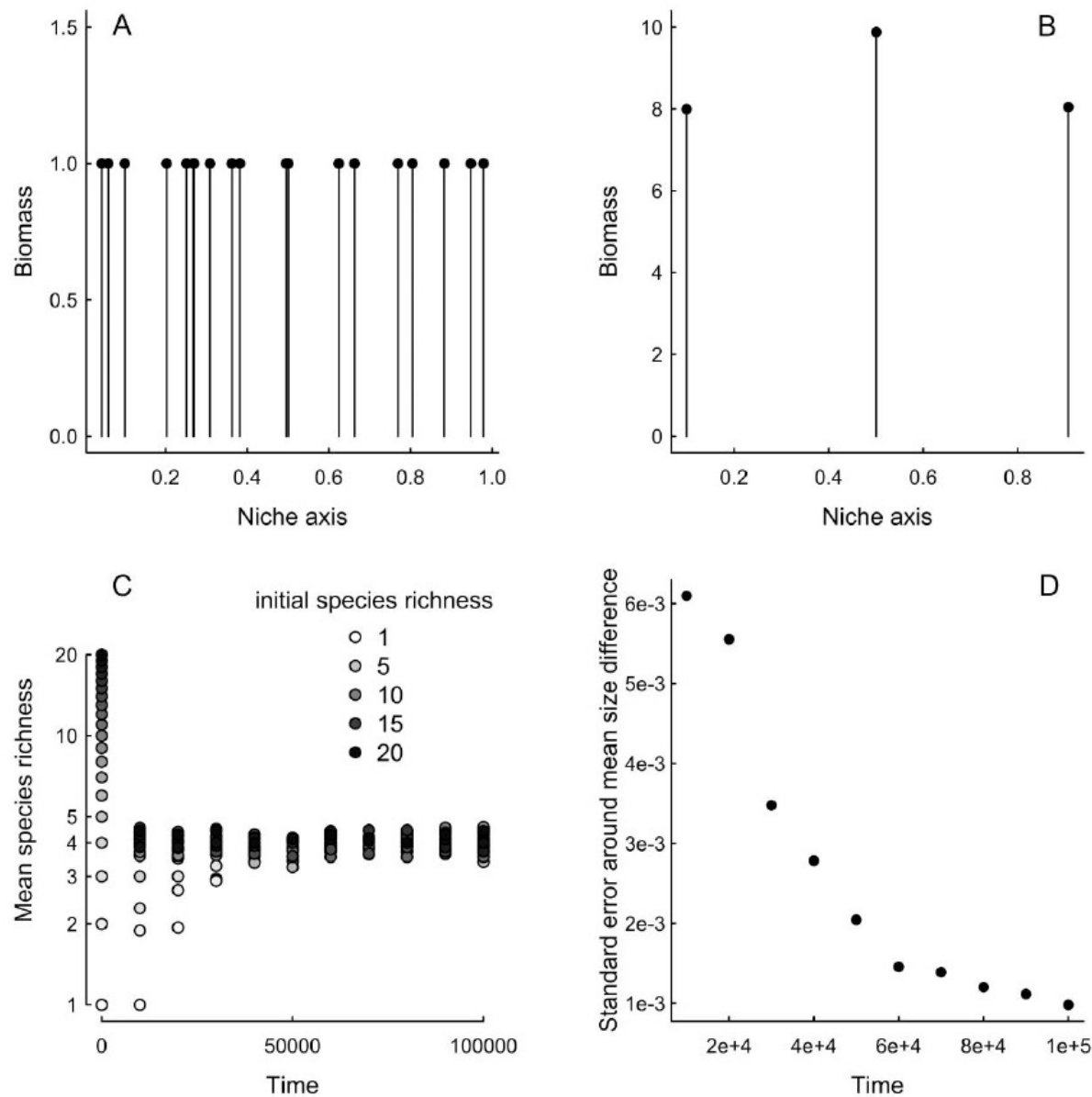


Figure 3: Evolution of subterranean beetle communities as simulated by the limiting-similarity model in the case of a point-mutation speciation process. *A*, *B*, Example of the evolution of a single simulated community under the limiting-similarity model from 20 species distributed at random to 3 dominant, evenly spaced species. *C*, Across 200 simulations, communities with a different initial species number ranging from 1 to 20 all converge on average toward a similar low number of species. Each of the three suitable size ranges that systematically emerges is occupied by one dominant species, sometimes accompanied by a few rarer ones. *D*, Distances between the three suitable size ranges progressively converge toward a unique value through time, and the standard deviation around dominant species' mean size differences decreases as a result.

Summary

- There is increasing sense that, as in population genetics, neutrality is a useful ecological null model
- There is an increasing sense that the realworld is some combination of niche & neutral processes
- By ignoring species differences, neutrality forces us to focus on local dispersal and regional species pools as drivers of local diversity.

“McGill and Nekola (2010) reach a similar conclusion, suggesting that of the three most important aspects of the neutral theory of biodiversity, neutrality appears dispensable, while dispersal limitation and the input of species from the metacommunity (regional replacement) appear to be critical in determining SADs for local communities.”

- Niche-neutrality goes a long way to explain Hutchinsonian ratios and the coexistence of lots of apparently similar species, inc the paradox of the plankton

References

Bell, G. 2001. Neutral Macroecology. *Science* **293**:2413-2418.

Hankin, R. K. S. 2007. Introducing untb, an R package for simulating ecological drift under the unified neutral theory of Biodiversity. *Journal of Statistical Software* **22**.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton.

Hutchinson, G. E. 1961. THE PARADOX OF THE PLANKTON. *American Naturalist* **95**:137-145.

Scheffer, M., and E. H. van Nes. 2006. Self-organized similarity, the evolutionary emergence of groups of similar species. *Proceedings of the National Academy of Sciences* **103**:6230-6235.

Scheffer M, Vergnon R, van Nes EH, Cuppen JGM, Peeters E, Leijds R, Nilsson AN. 2015. The Evolution of Functionally Redundant Species; Evidence from Beetles. *Plos One* **10**: 10.

Scheffer M, van Nes EH and Vergnon R. (2018) Toward a unifying theory of biodiversity. *Proc Natl Acad Sci U S A* **115**, 639-641.

Vergnon, R., N. K. Dulvy, and R. P. Freckleton. 2009. Niches versus neutrality: uncovering the drivers of diversity in a species-rich community. *Ecology Letters* **12**:1079-1090.

Vergnon R, Leijds R, van Nes EH, Scheffer M. 2013. Repeated parallel evolution reveals limiting similarity in subterranean diving beetles. *Am Nat* **182**: 67-75.

Whittaker plot shapes for a range of niche partitioning models

