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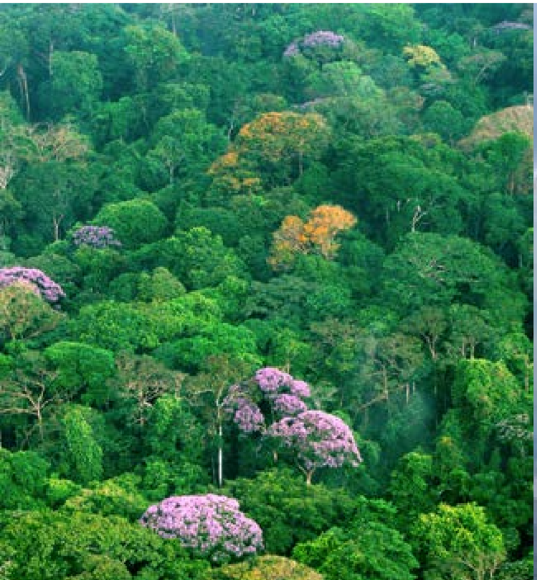
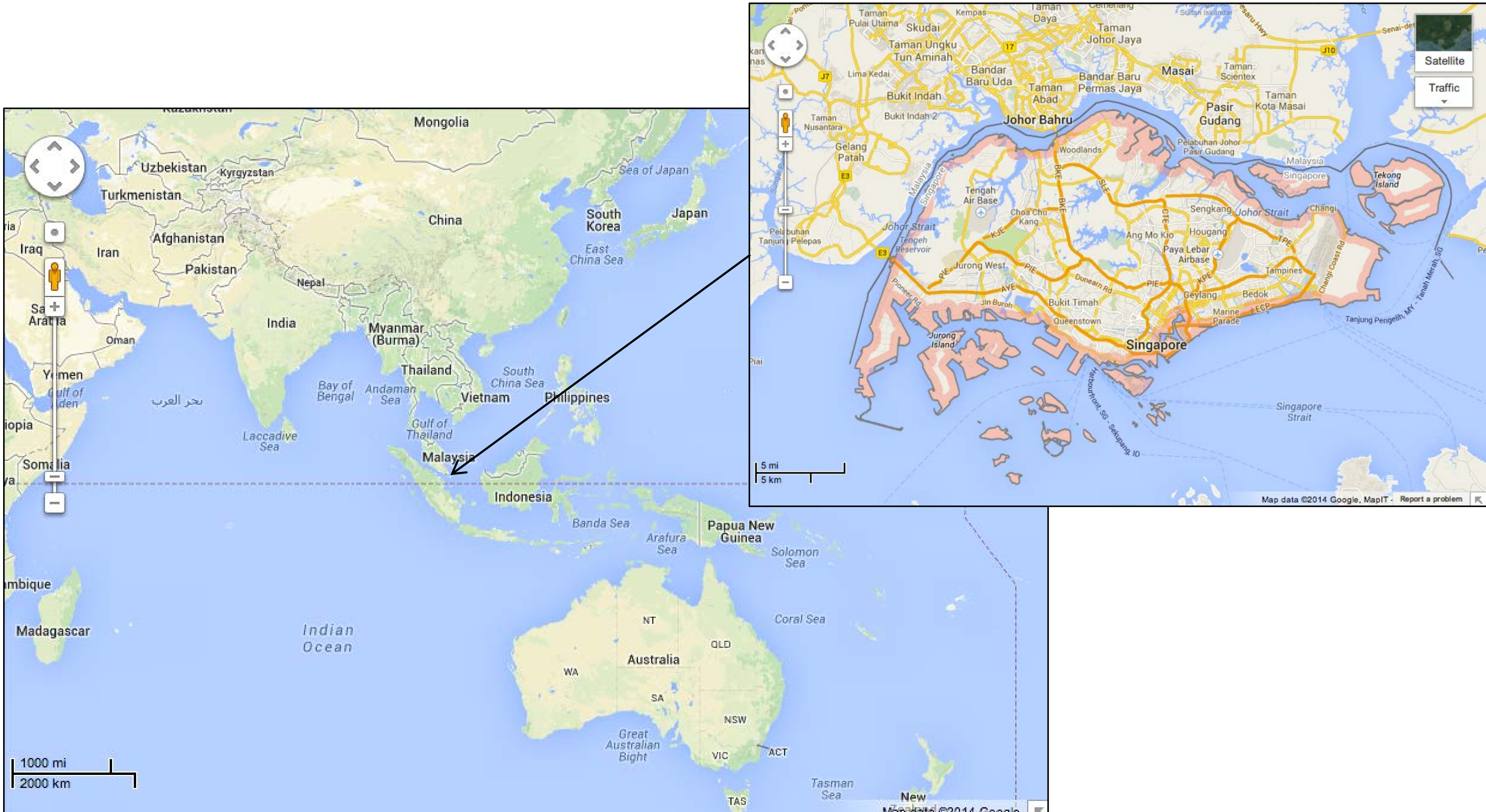
A unified theory of niche assembly and dispersal assembly in community ecology

Ryan Chisholm



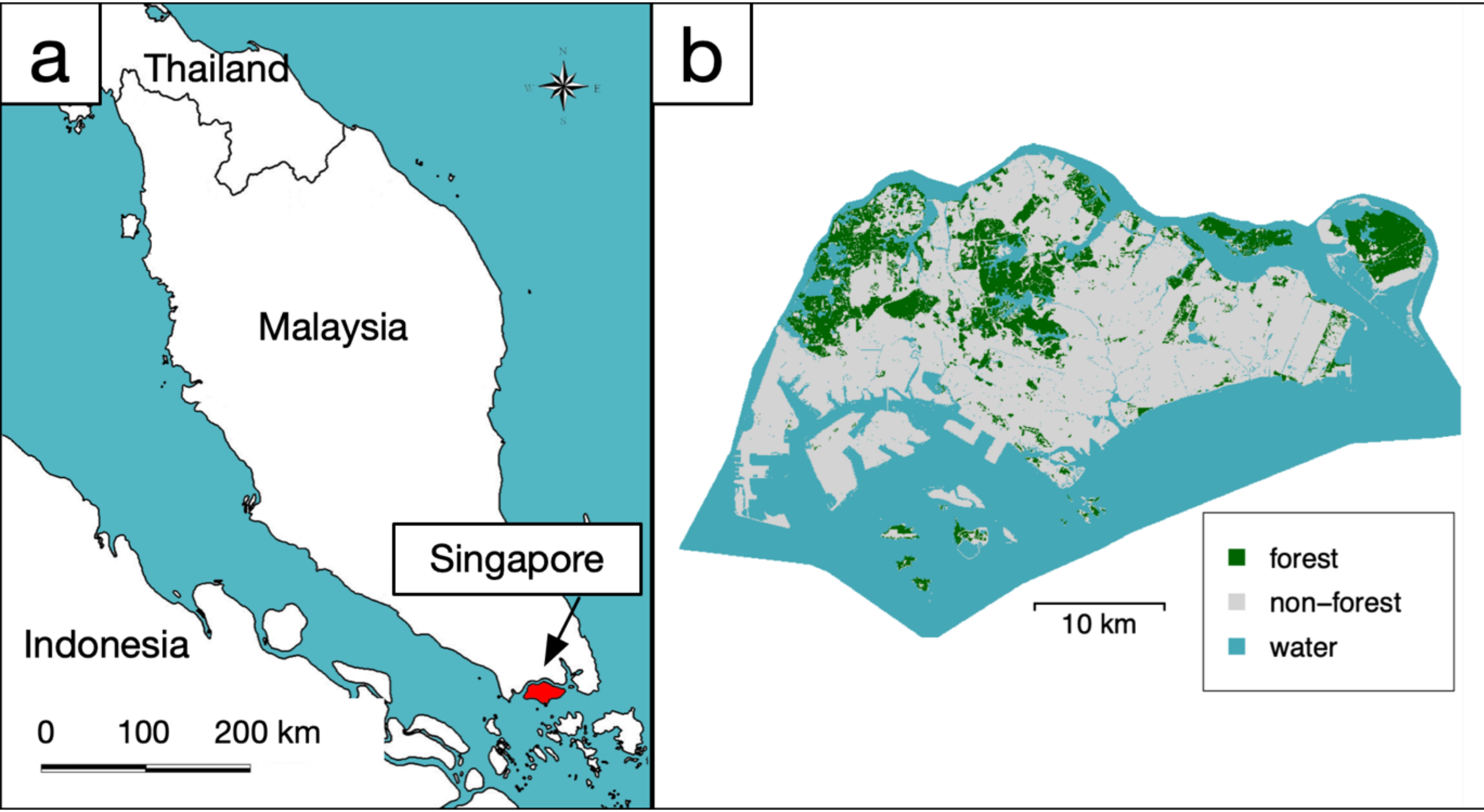
Singapore



Mongolia
Uzbekistan
Kyrgyzstan
Turkmenistan
China
Sea of Japan
South Korea
Japan
Iraq
Iran
Afghanistan
Pakistan
Nepal
East China Sea
India
Oman
Myanmar (Burma)
Thailand
South China Sea
Bay of Bengal
Andaman Sea
Vietnam
Philippines
بحر العرب
Gulf of Thailand
Laccadive Sea
Malaysia
Indonesia
Banda Sea
Arafura Sea
Papua New Guinea
Solomon Sea
Madagascar
Indian Ocean
Coral Sea
NT
QLD
Australia
WA
SA
NSW
Great Australian Bight
VIC
ACT
TAS
Tasman Sea
New
1000 mi
2000 km
Map data ©2014 Google
Skudai
Taman Ungku Tun Aminah
Taman Johor Jaya
Bandar Baru Uda
Taman Abad
Bandar Baru Permas Jaya
Masai
Bukit Indah
Johor Bahru
Pasir Gudang
Taman Kota Masai
Gelang Patah
Woodlands
Tengah Air Base
Johor Strait
Sengkang
Ang Mo Kio
Hougang
Paya Lebar Airbase
Jurong West
Tampines
Changi
Tekong Island
Bukit Timah
Geylang
Bedok
Marine Parade
Queenstown
Singapore
Jurong Island
Singapore Strait
5 mi
5 km
Satellite
Traffic
Map data ©2014 Google, MapIT
Report a problem

Singapore

- City-state
- Former British colony
- Area: 719 km^2
- Population: 6 million (~30% foreigners)
- Languages: English, Malay, Chinese, Tamil


a
Thailand
Malaysia
Indonesia
Singapore
0
100
200 km
b
forest
non–forest
water
10 km







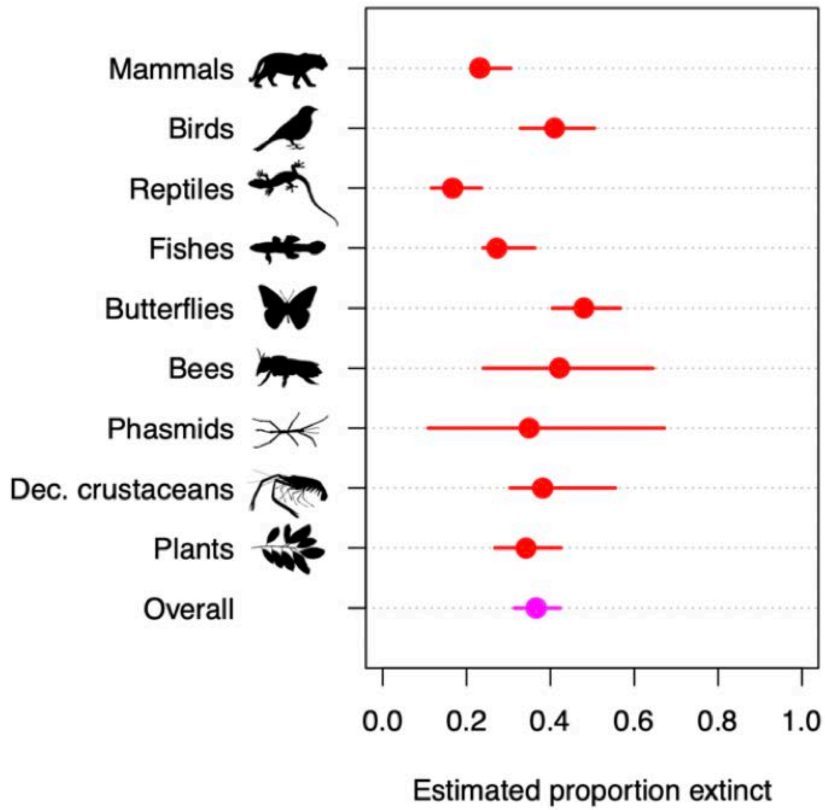



VILLAGE

Taxonomic group	Number of species	Number of records
Mammals	32	64
Birds	154	3847
Reptiles	121	2925
Amphibians	25	1132
Fishes	46	676
Butterflies	413	7108
Bees	129	239
Phasmids	46	258
Decapod crustaceans	23	205
Plants	2076	34224
Total	3065	50678

Two centuries of deforestation and biodiversity loss in Singapore

Ryan A. Chisholm, Nadiah P. Kristensen, Frank E. Rheindt, Kwek Yan Chong, John S. Ascher, Kelvin K. P. Lim, Peter K. L. Ng, Darren C. J. Yeo, Rudolf Meier, Heok Hui Tan, Xingli Giam, Yi Shuen Yeoh, Wei Wei Seah, Laura M. Berman, Hui Zhen Tan, Keren R. Sadanandan, Meryl Theng, Wan F. A. Jusoh, Anuj Jain, Blanca Huertas, David J. X. Tan, Alicia C. R. Ng, Aloysius Teo, Zeng Yiwen, Tricia Cho, & Y. C. Keita Sin



What maintains the diversity of local ecological communities?

Two broad possibilities:

- Niches
- Dispersal

Ecology, 62(3), 1981, pp. 802–815
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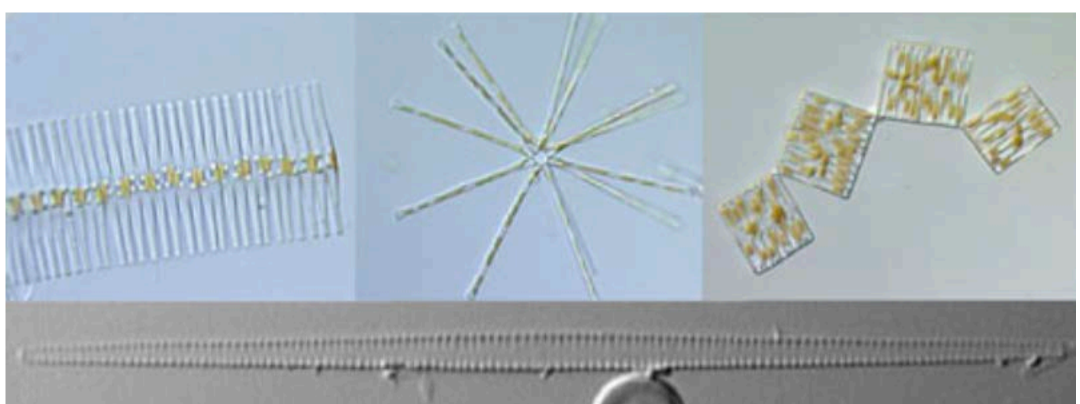
TESTS OF RESOURCE COMPETITION THEORY USING FOUR SPECIES OF LAKE MICHIGAN ALGAE[1]

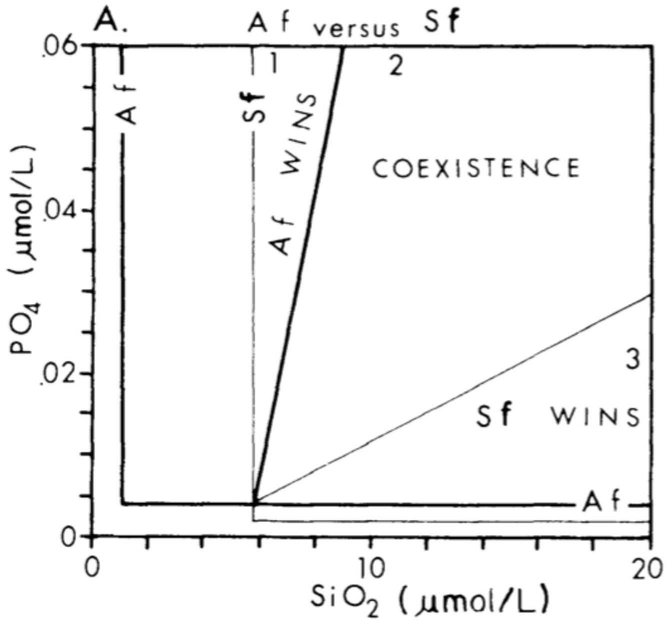
DAVID TILMAN
Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, Minnesota 55455 USA

Abstract. The results of nutrient competition experiments performed for all the pairwise combinations of four species of freshwater algae often agreed with the predictions of a graphical model of resource competition. As predicted by theory, the species with the significantly lower resource requirement, as measured by R^*, was the superior competitor when both species were limited by the same resource. Two species were observed to coexist only if either (1) each was limited by a different resource and met the theoretical criteria for coexistence or (2) the species were limited by the same resource and did not differ significantly in their resource requirements.

Single-species experiments were used to determine the functional dependence of the growth rate of each Lake Michigan diatom species on the concentration of limiting silicate or phosphate. The results, fit to the Monod (Michaelis-Menten) model, predicted that *Fragilaria crotonensis* and *Asterionella formosa* had identical silicate requirements, and that both were silicate competitors superior to *Synedra filiformis* and *Tabellaria flocculosa*. The phosphate requirements of the four species were very similar, with *Synedra* requiring significantly less phosphate than *Tabellaria*. Competition experiments demonstrated that *Tabellaria* was competitively displaced by the three other species for all silicate-to-phosphate ratios, as predicted. *Asterionella* and *Fragilaria* were apparently competitively equal, coexisting for all silicate-to-phosphate ratios used, suggesting evolution of similar resource requirements by these two commonly dominant species. *Asterionella* and *Synedra* coexisted for intermediate silicate-to-phosphate ratios, as did *Synedra* and *Fragilaria*.

Key words: competition; diatoms; functional response; Lake Michigan; Monod model; phosphate; resource competition; silicate.



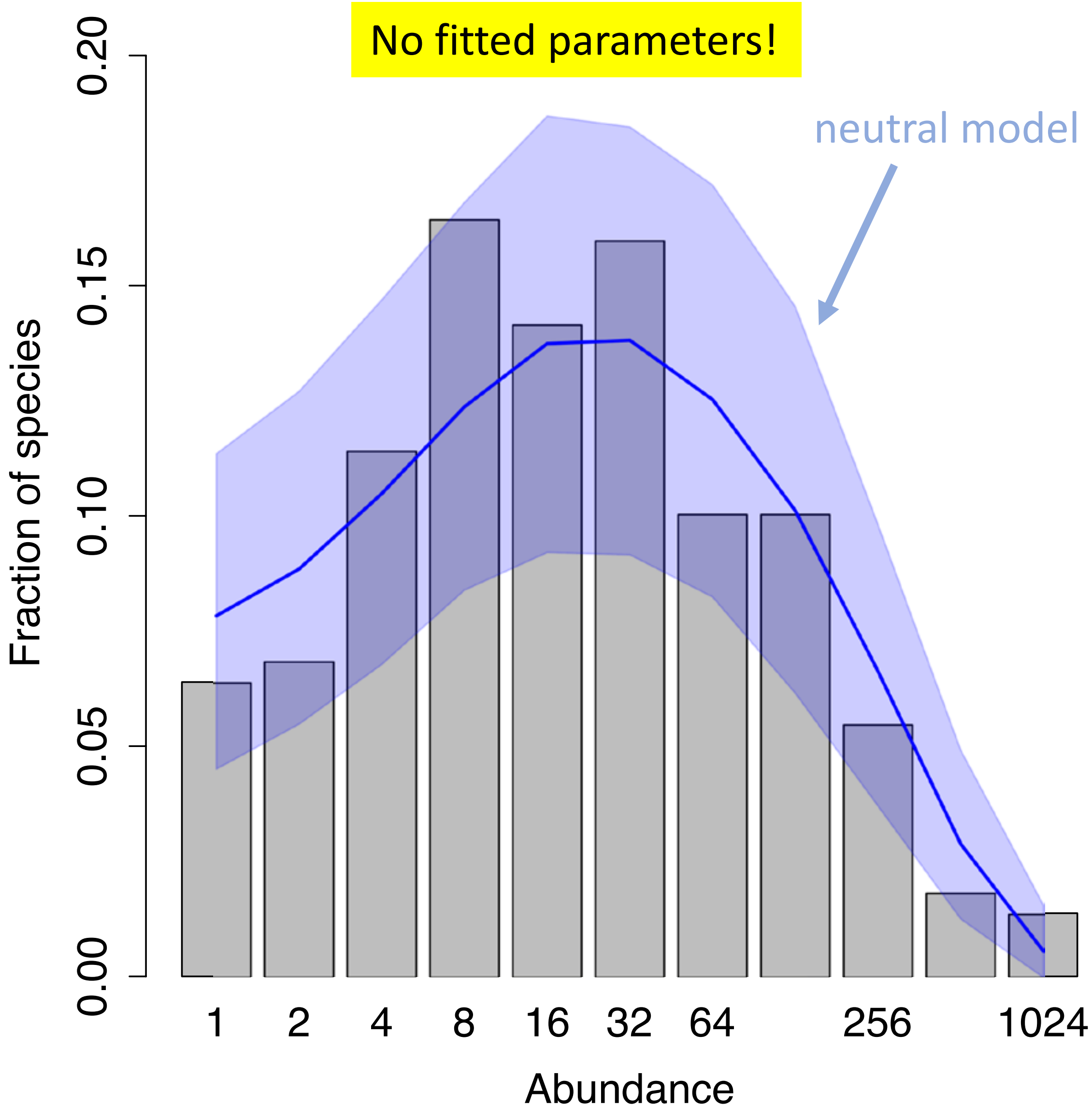


Tilman 1981 *Ecology*

The Unified Neutral Theory of
BIODIVERSITY AND BIOGEOGRAPHY

STEPHEN P. HUBBELL

MONOGRAPHS IN POPULATION BIOLOGY • 32

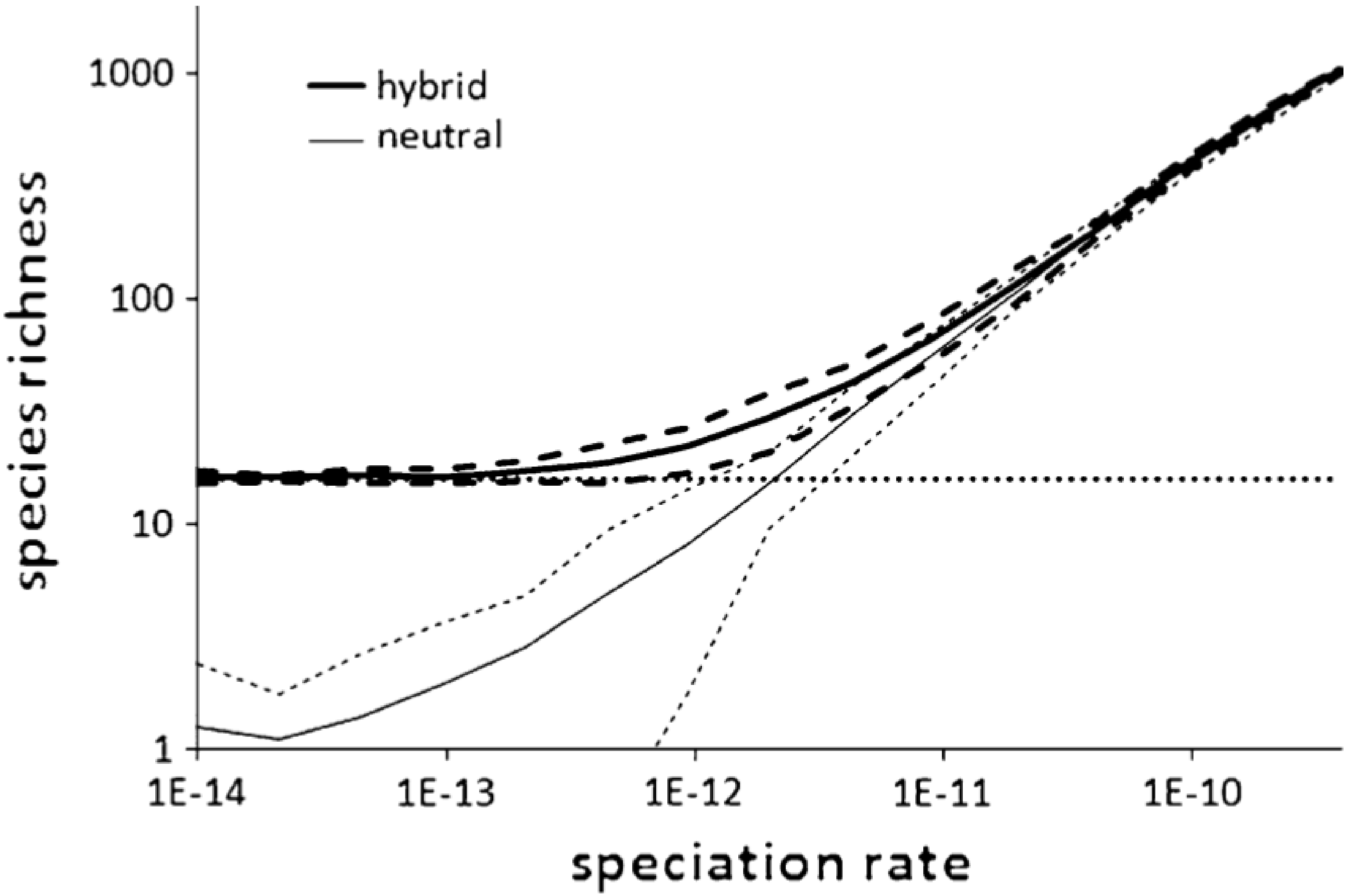


Chisholm & Pacala 2010 *PNAS*; Chisholm 2025 in *The First 100 Years of Research on Barro Colorado Island*

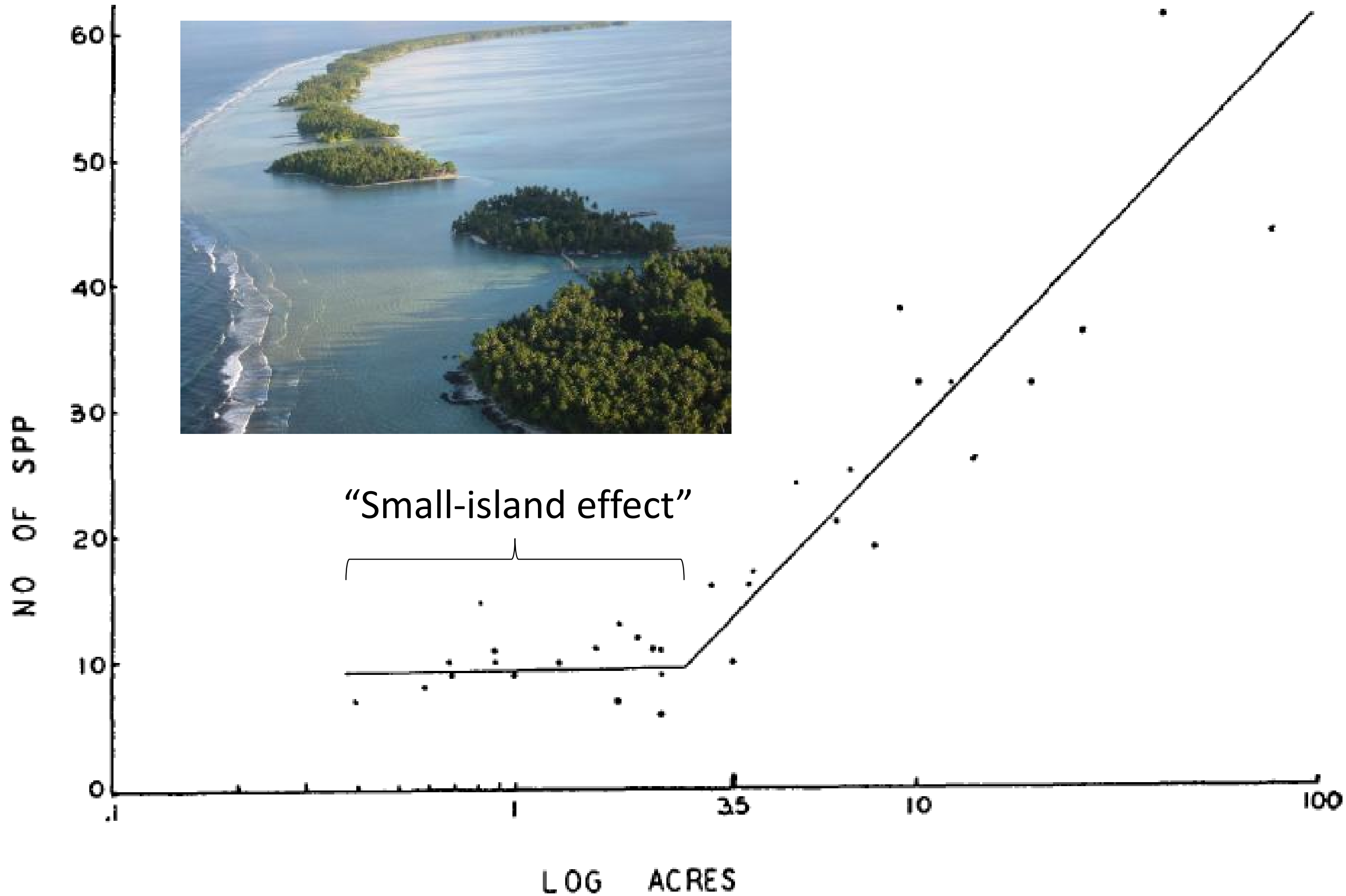
What maintains the diversity of local ecological communities?

Two broad possibilities:

- Niches → niche-assembly theory
- Dispersal → dispersal-assembly theory (neutral theory, mass effects, source–sink dynamics, etc.)



Purves & Pacala 2005 in *Biotic Interactions in the Tropics*; Chisholm & Pacala 2010 *PNAS*; Chisholm & Pacala 2011 *Theoretical Ecology*



Niering 1963 *Ecological Monographs*; MacArthur & Wilson 1967 *The Theory of Island Biogeography*

Area = A = 100

Niches = n^* = 4

Area = A = 100

Niches = n^* = 4

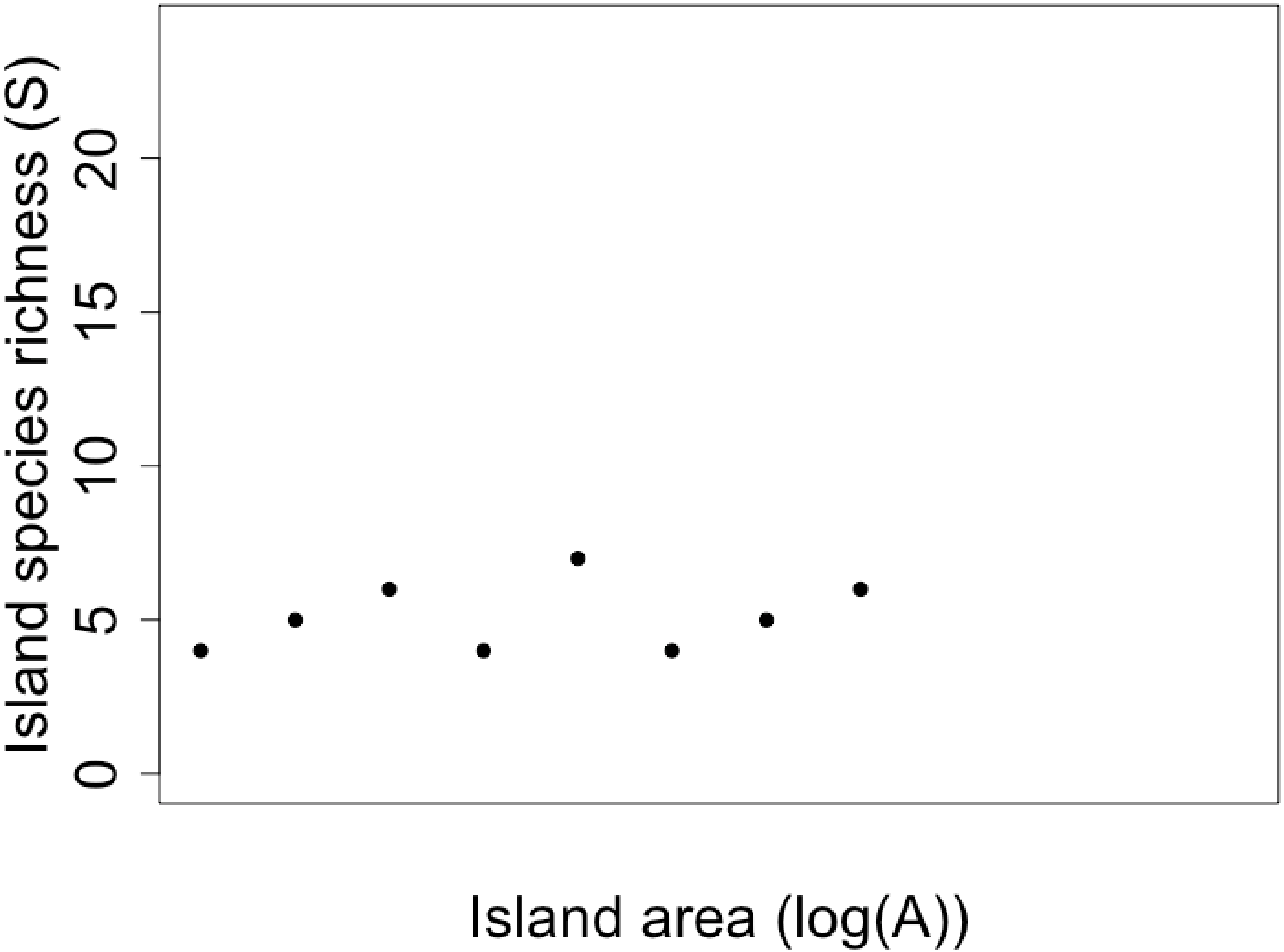
Species richness = $S \sim n^* = 4$

$A = 200$

$S \sim n^* = 4$

$A = 250$

$S \sim n^* = 5$



Island species richness (S)
0
5
10
15
20
Island area (log(A))

$A = 400$

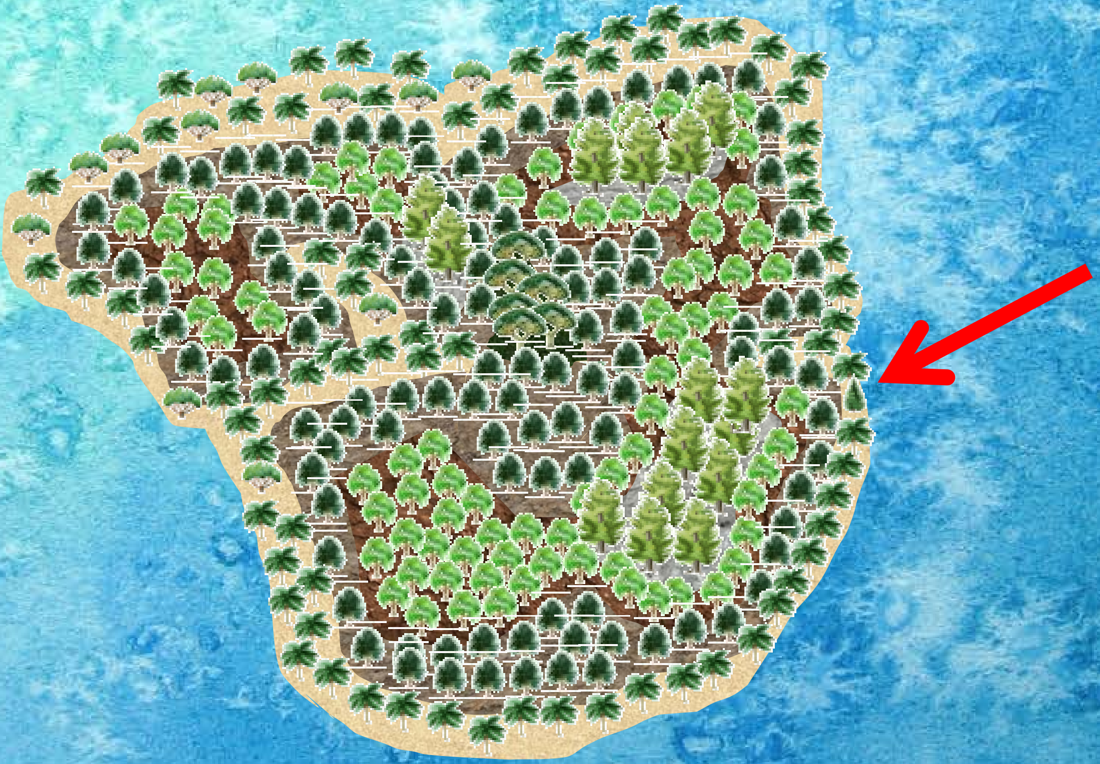
$n^* = 5$

$A = 400$
$n^* = 5$
$S = 6$

$A = 400$

$n^* = 5$

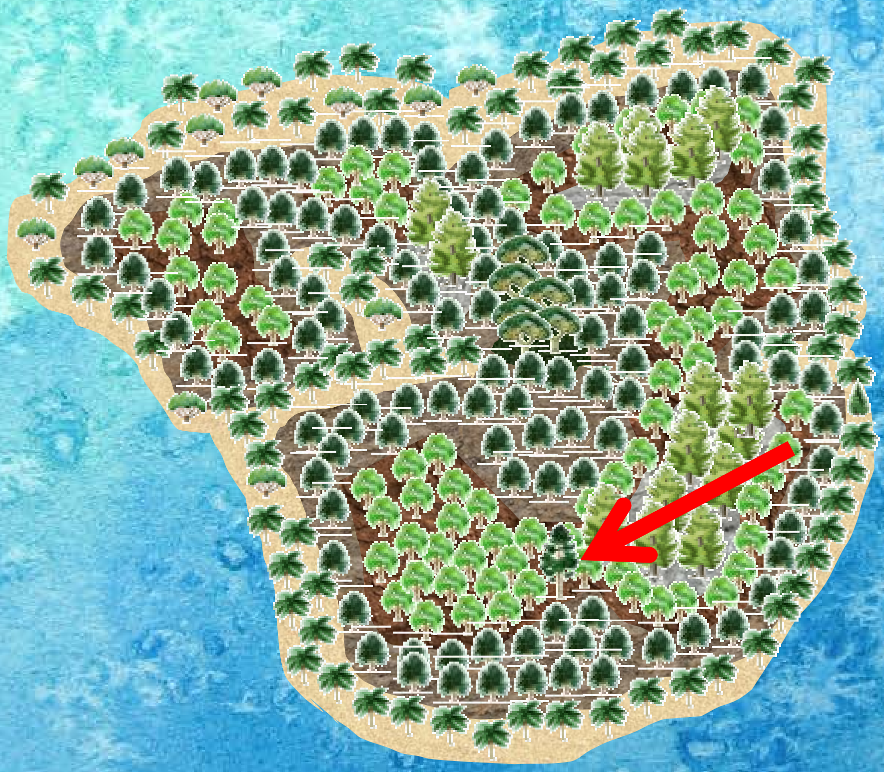
$S = 7$



$A = 400$

$n^* = 5$

$S = 8$



$A = 800$

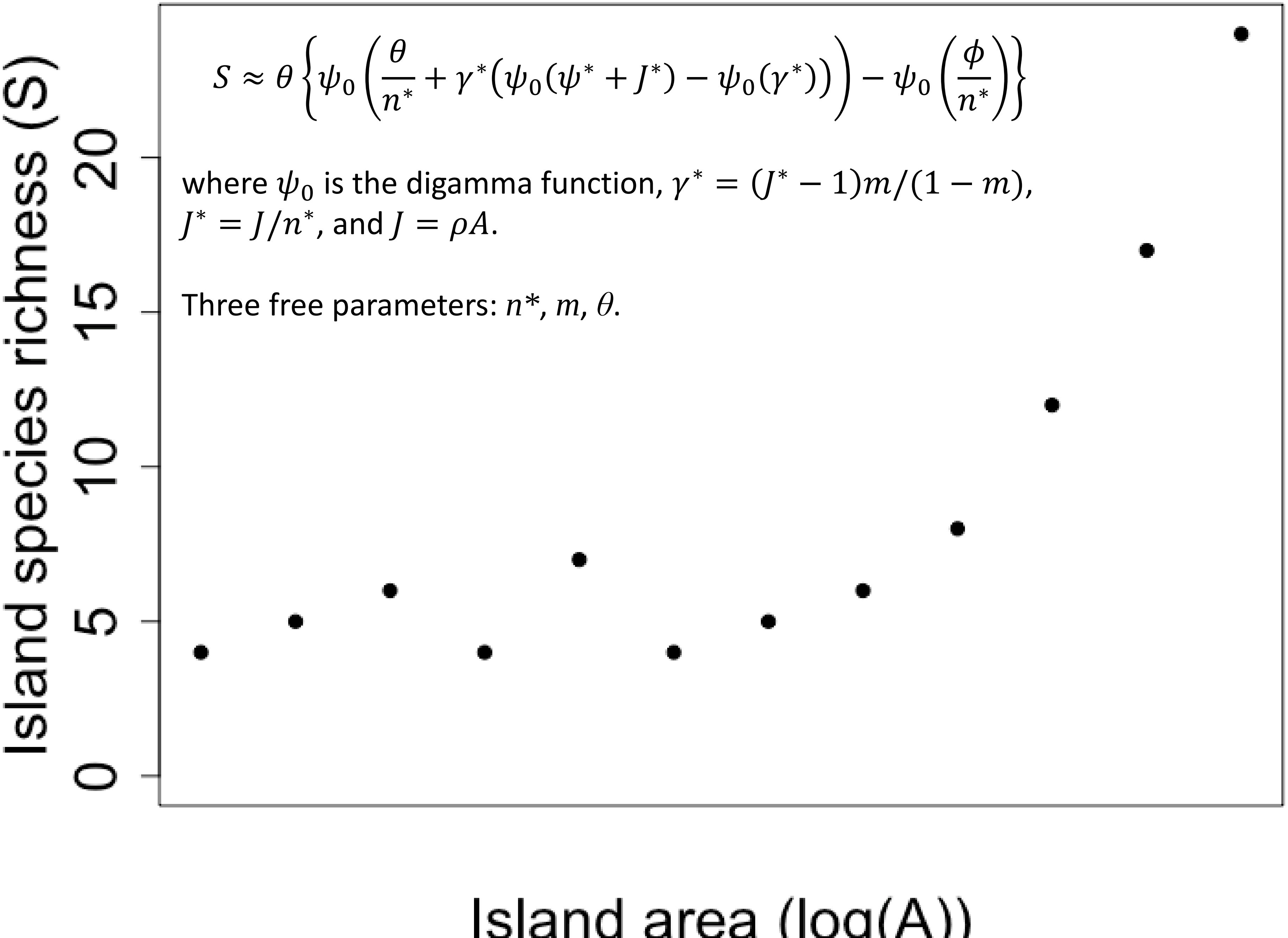
$n^* = 5$

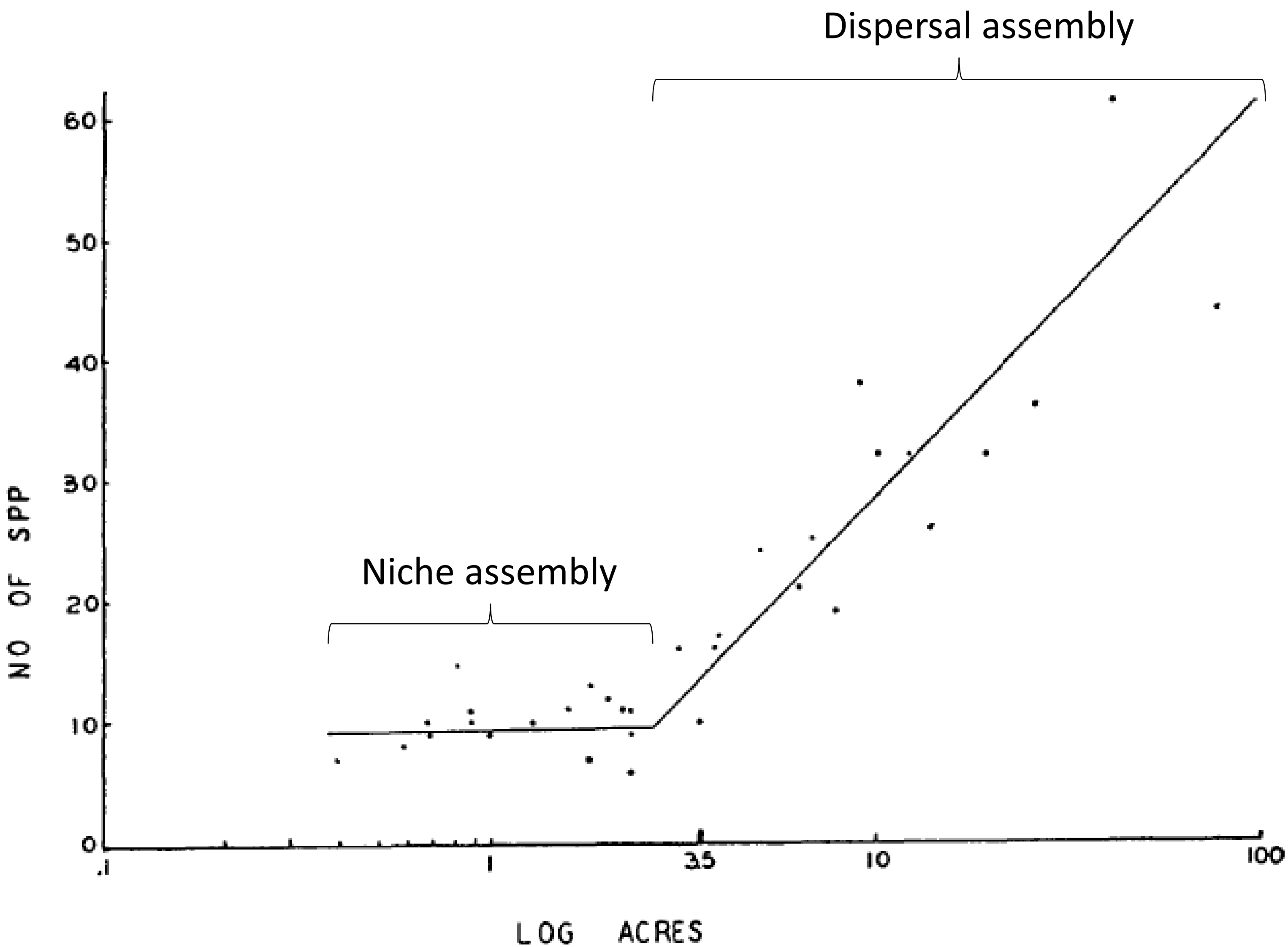
$S = 10$

$$S \approx \theta \left\{ \psi_0 \left(\frac{\theta}{n^*} + \gamma^* \left(\psi_0(\psi^* + J^*) - \psi_0(\gamma^*) \right) \right) - \psi_0 \left(\frac{\phi}{n^*} \right) \right\}$$

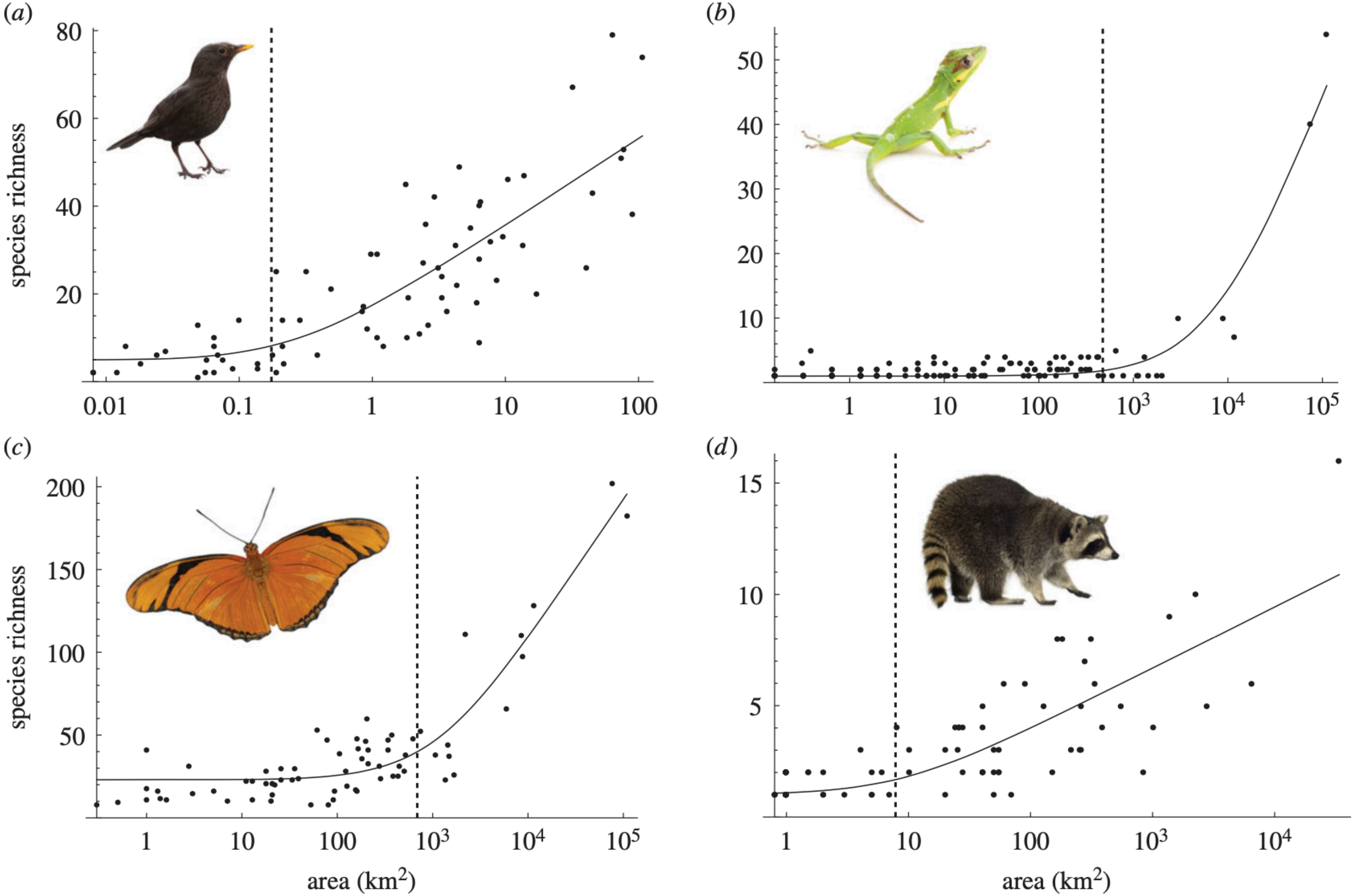
where ψ_0 is the digamma function, $\gamma^* = (J^* - 1)m/(1 - m)$, $J^* = J/n^*$, and $J = \rho A$.

Three free parameters: n^*, m, θ.





Niering 1963 *Ecological Monographs*; MacArthur & Wilson 1967 *The Theory of Island Biogeography*



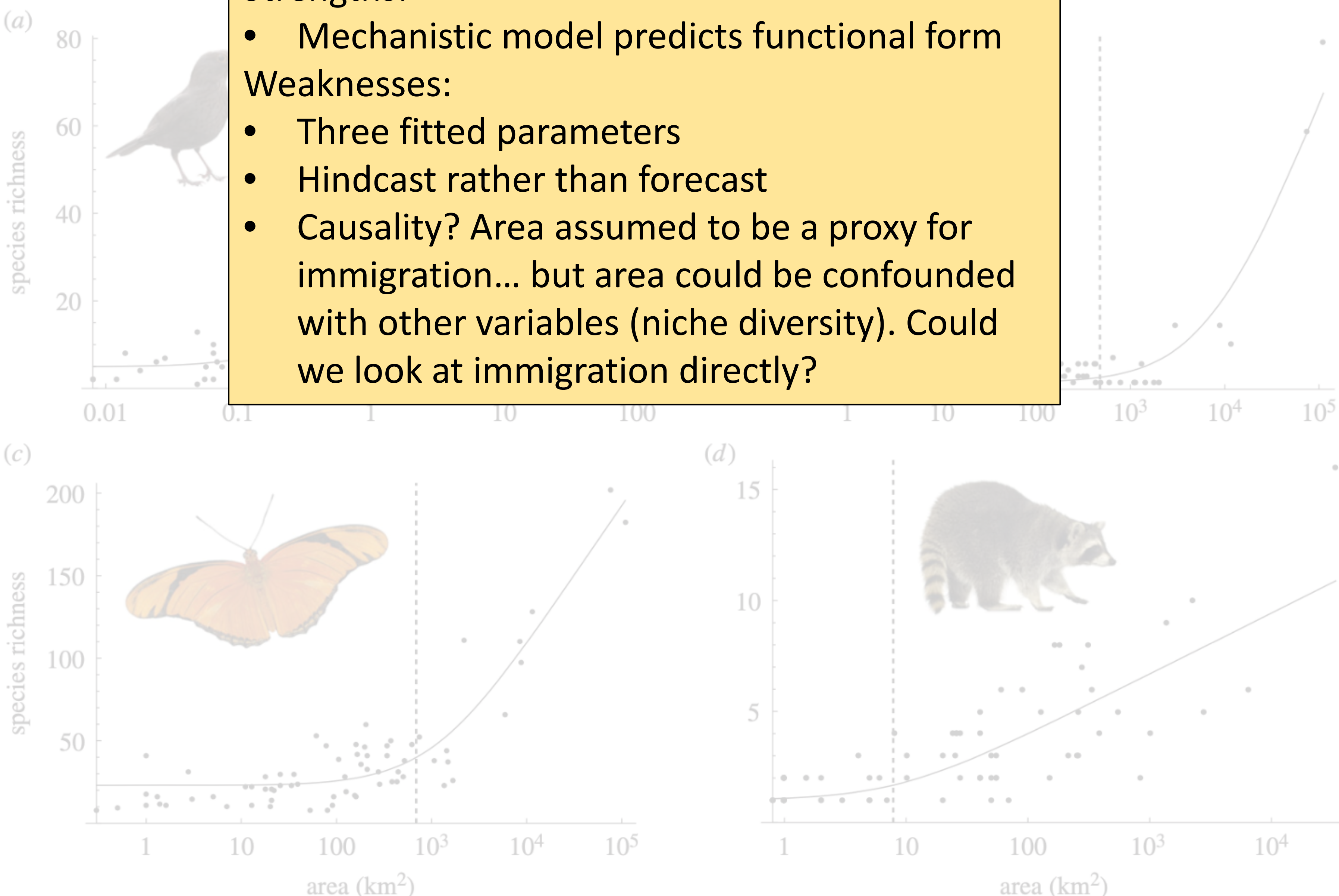
Chisholm *et al.* 2016 *Proceedings of the Royal Society B*

Strengths:

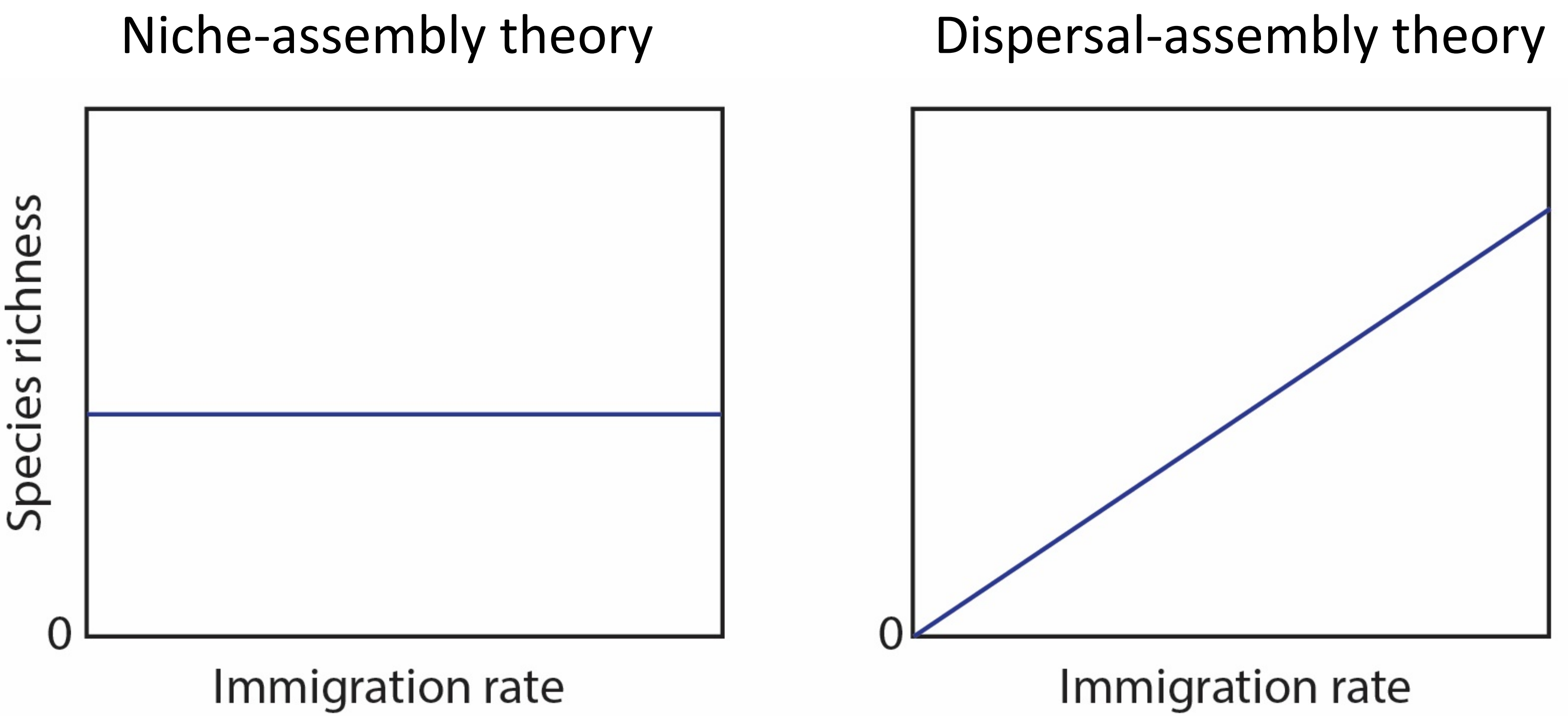
- Mechanistic model predicts functional form

Weaknesses:

- Three fitted parameters
- Hindcast rather than forecast
- Causality? Area assumed to be a proxy for immigration… but area could be confounded with other variables (niche diversity). Could we look at immigration directly?

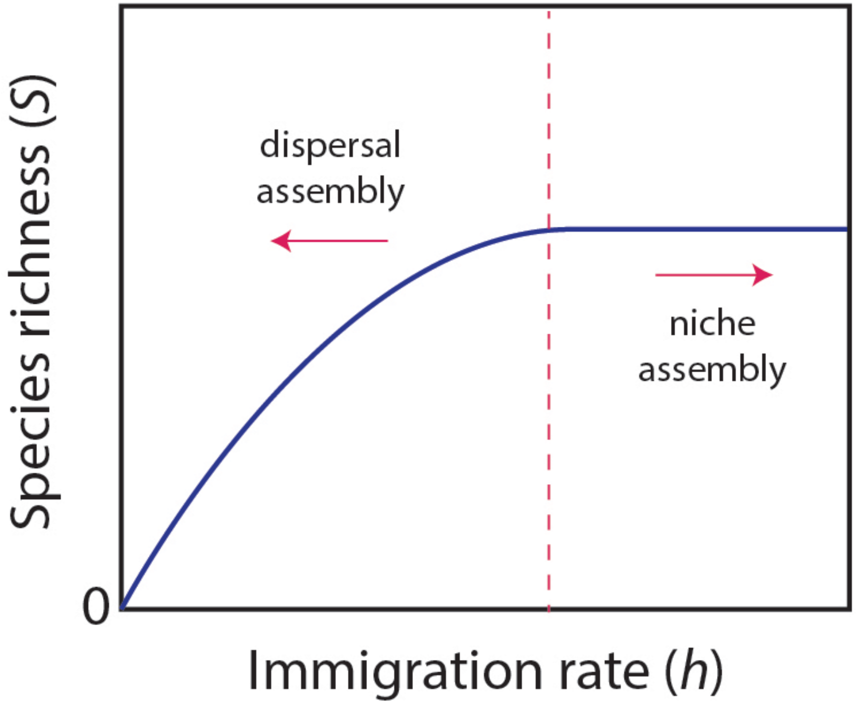


Species richness versus immigration



Species richness versus immigration

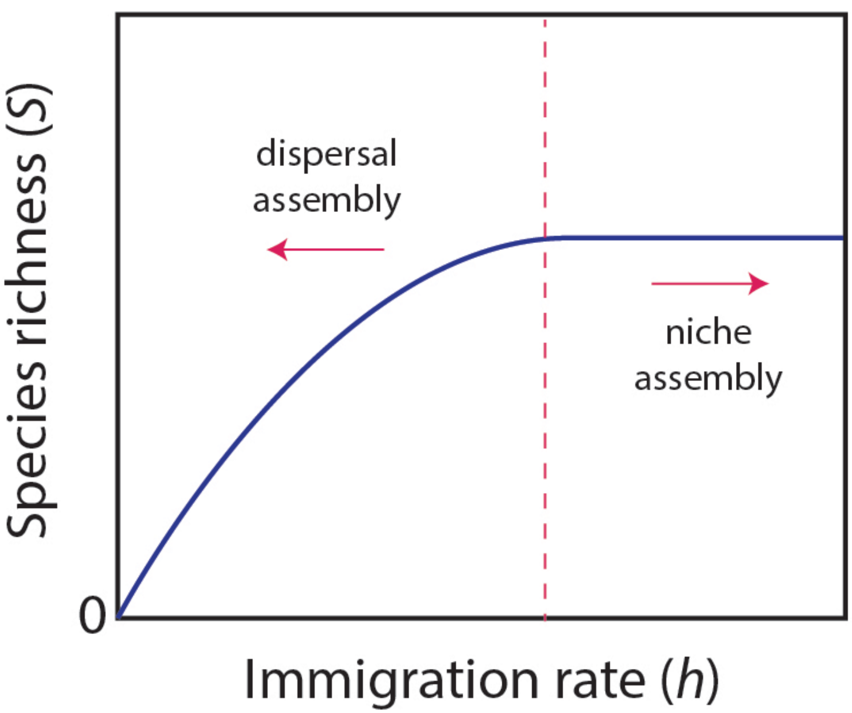
Classic unified theory
(MacArthur & Wilson)

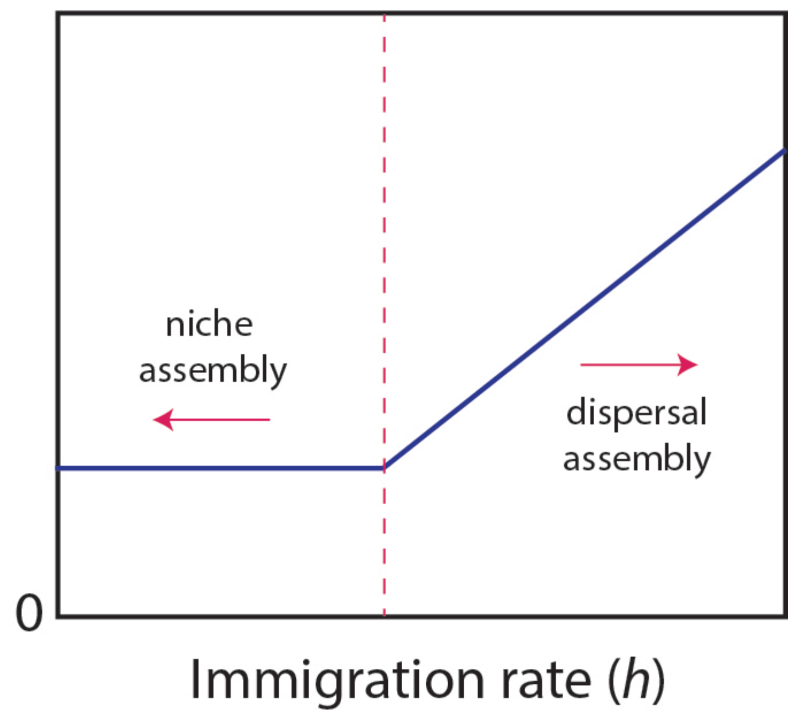


Species richness versus immigration

Classic unified theory
(MacArthur & Wilson)

Novel unified theory





Chisholm & Fung 2021 *Theoretical Ecology*

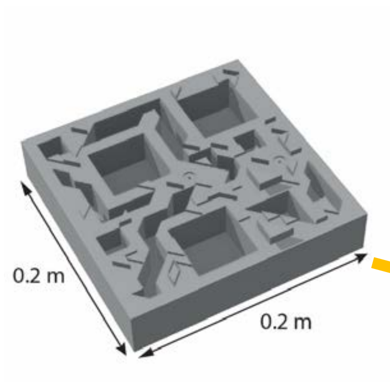
Species richness versus immigration

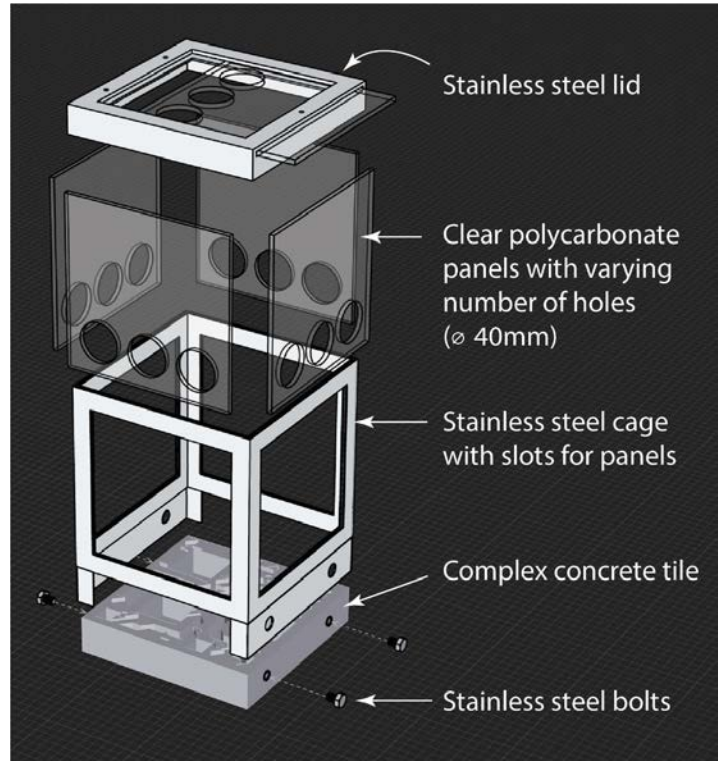
Lynette Loke

Species richness versus immigration

One treatment replicate:

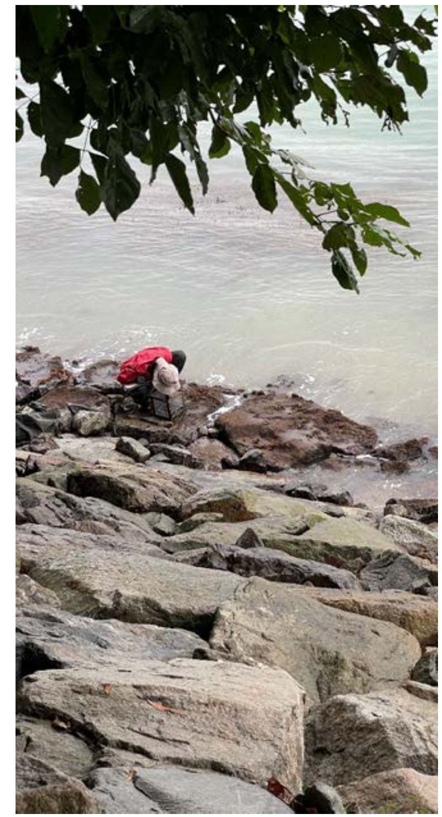
1) Habitat tile
2) Custom-built stainless-steel cage





12 treatments (numbers of holes) × 5 replicates = 60 units
Units were completely submerged ~95% of the time.

Species richness versus immigration



Species richness versus immigration

Classic unified theory
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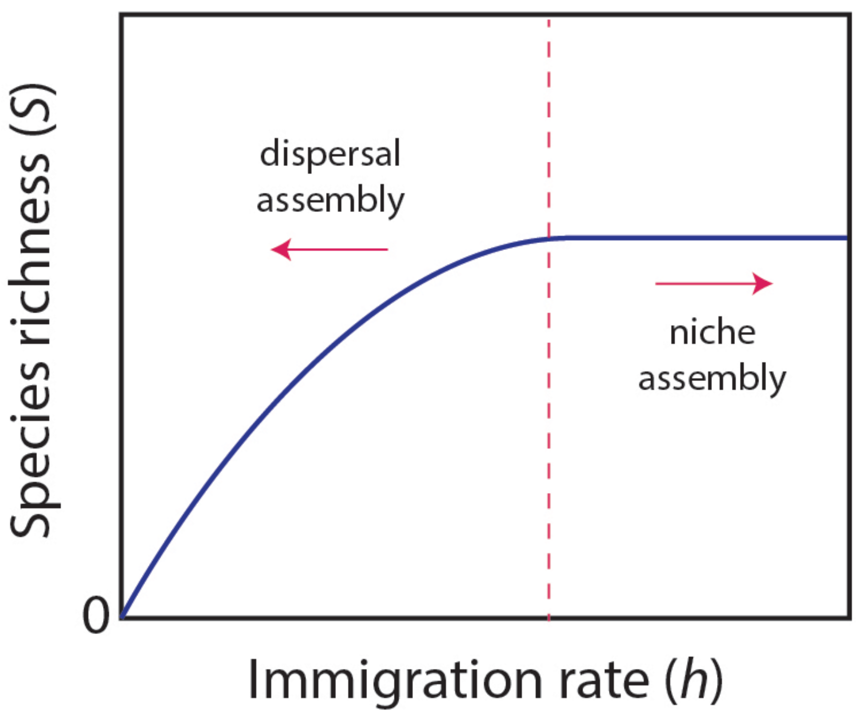
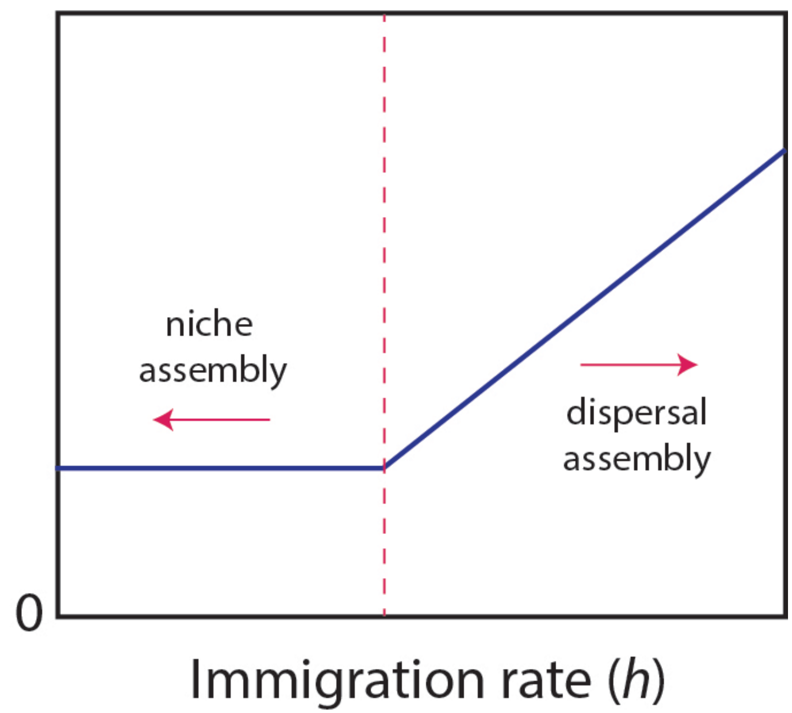
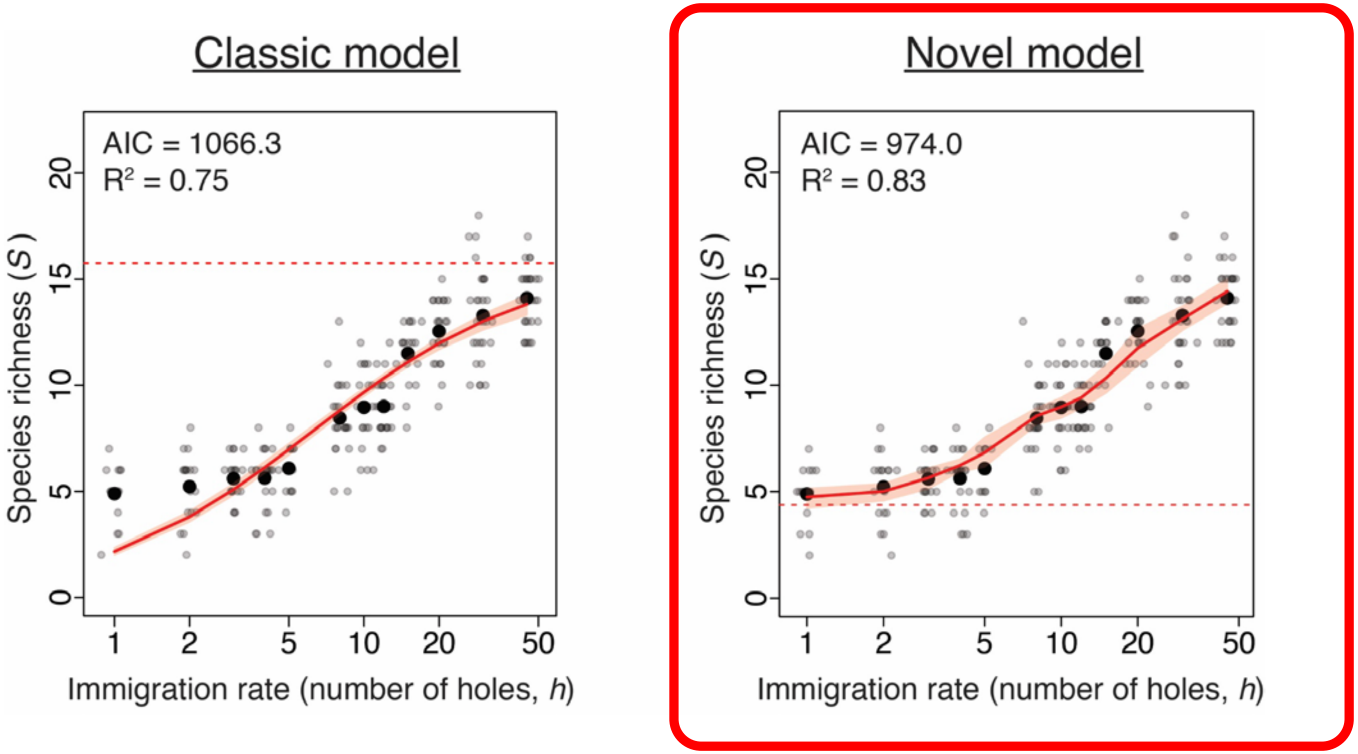


Novel unified theory



Species richness versus immigration



Loke & Chisholm 2023 *Nature*

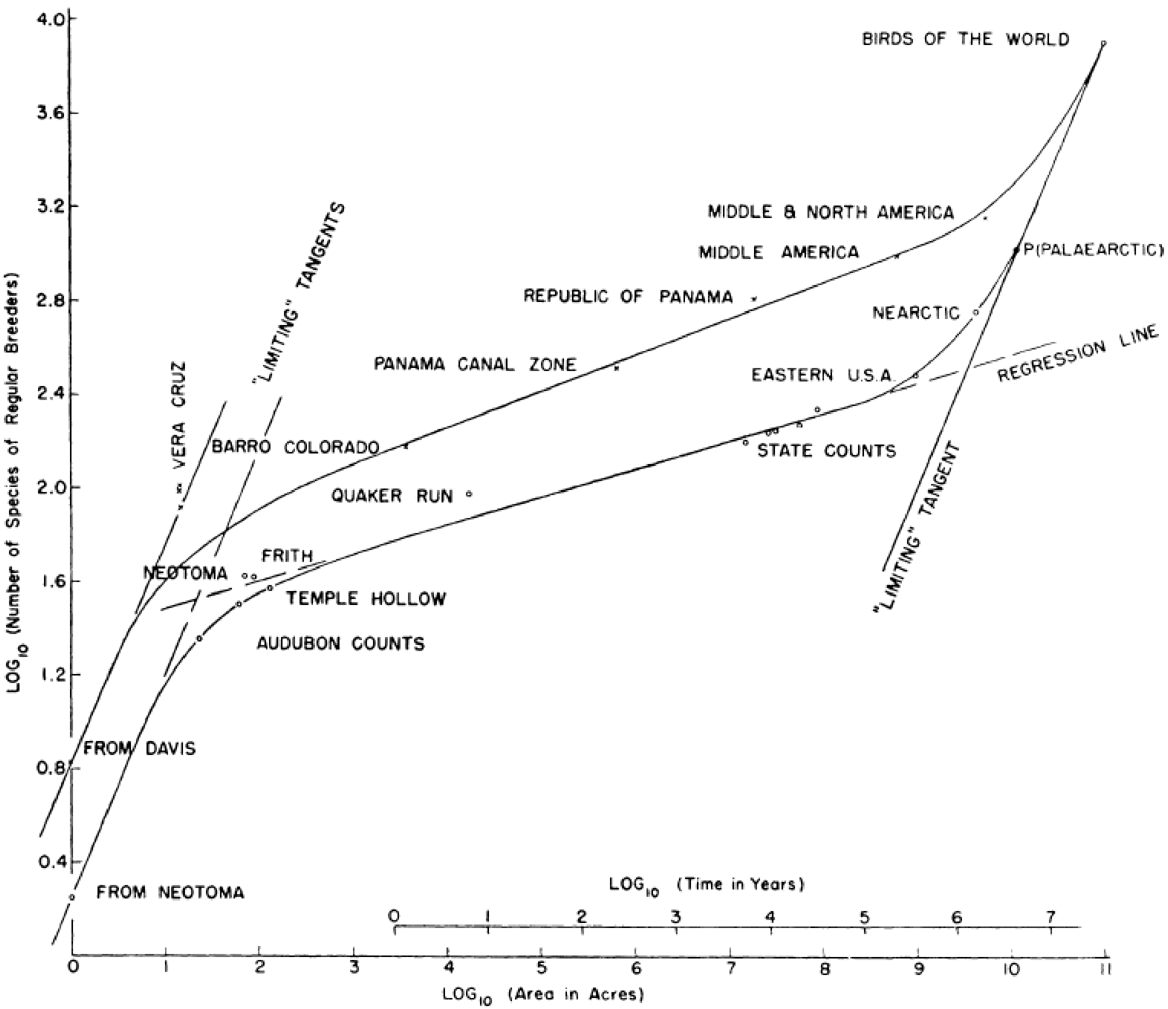
Strengths:

- A true prediction
- Predicts functional form
- Could have been substantially wrong—risky experiment

Weaknesses:

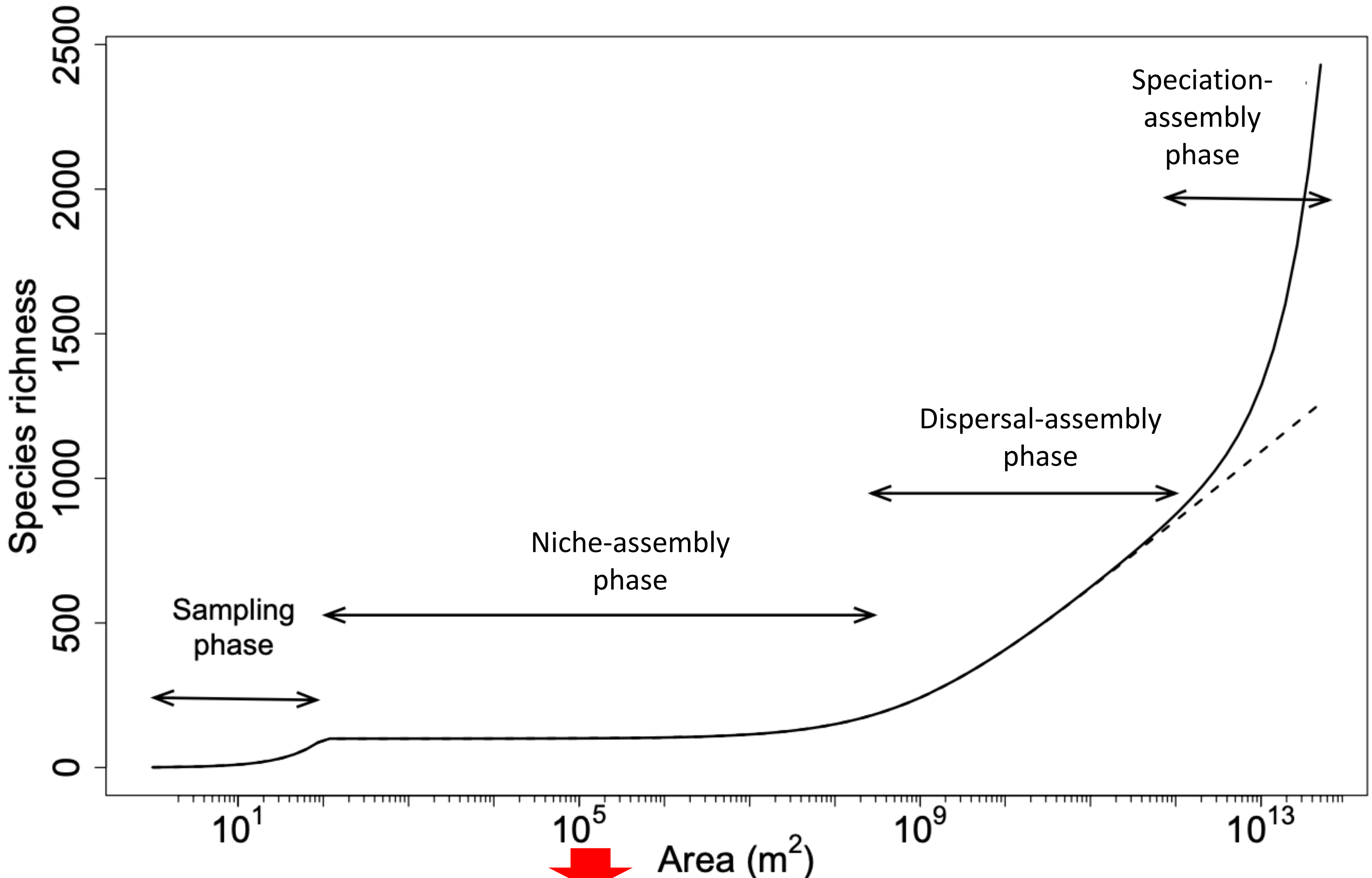
- Model still has three fitted parameters
- Only one pattern

Species–area relationship



Preston 1960 *Ecology*

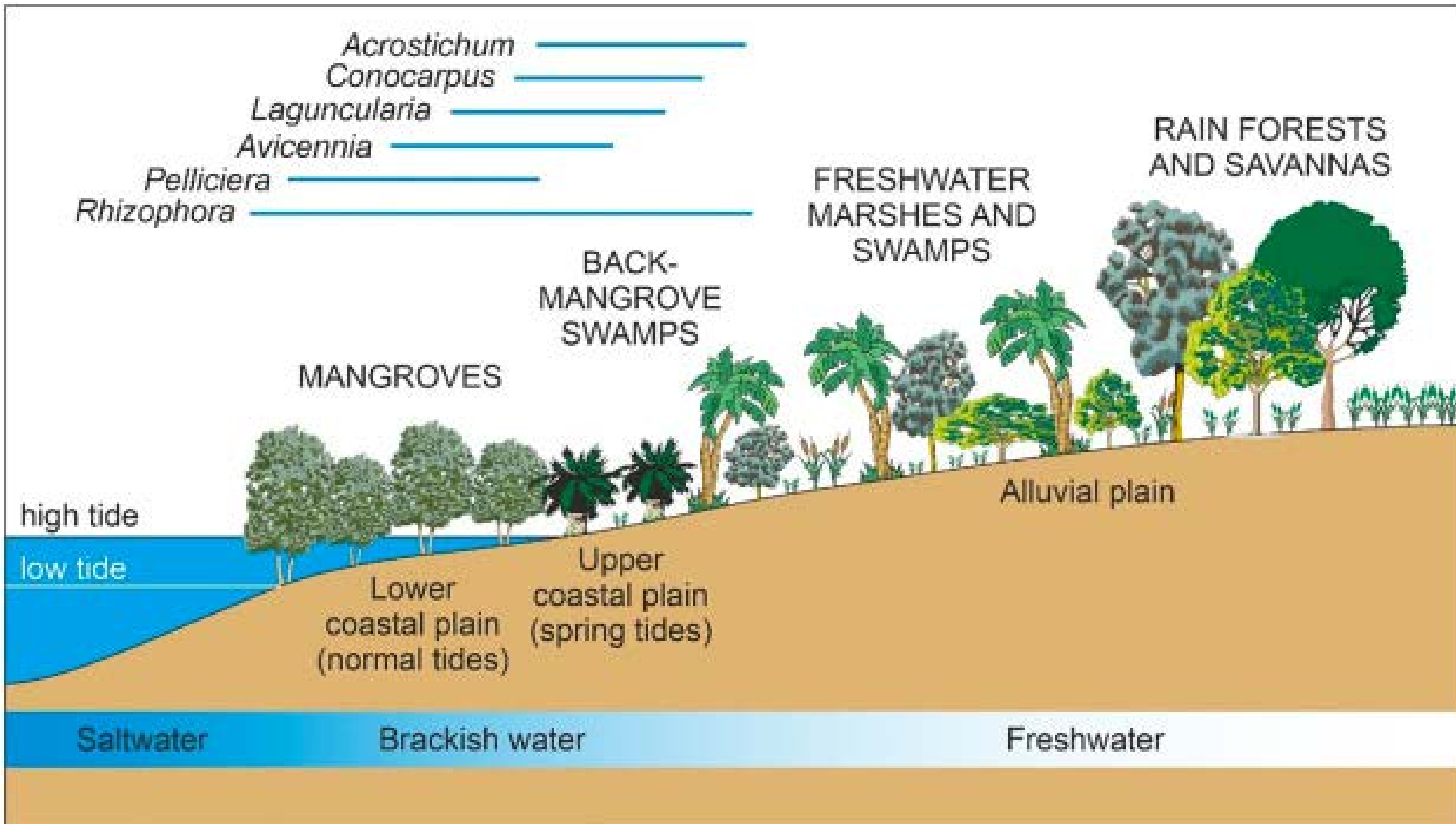
Can we reconcile the classic triphasic mainland species–area relationship with the island species–area relationship and the "small-island effect"?



Prediction: should observe previously unseen flat niche-structured phase in the species–area relationship in systems with low metacommunity diversity

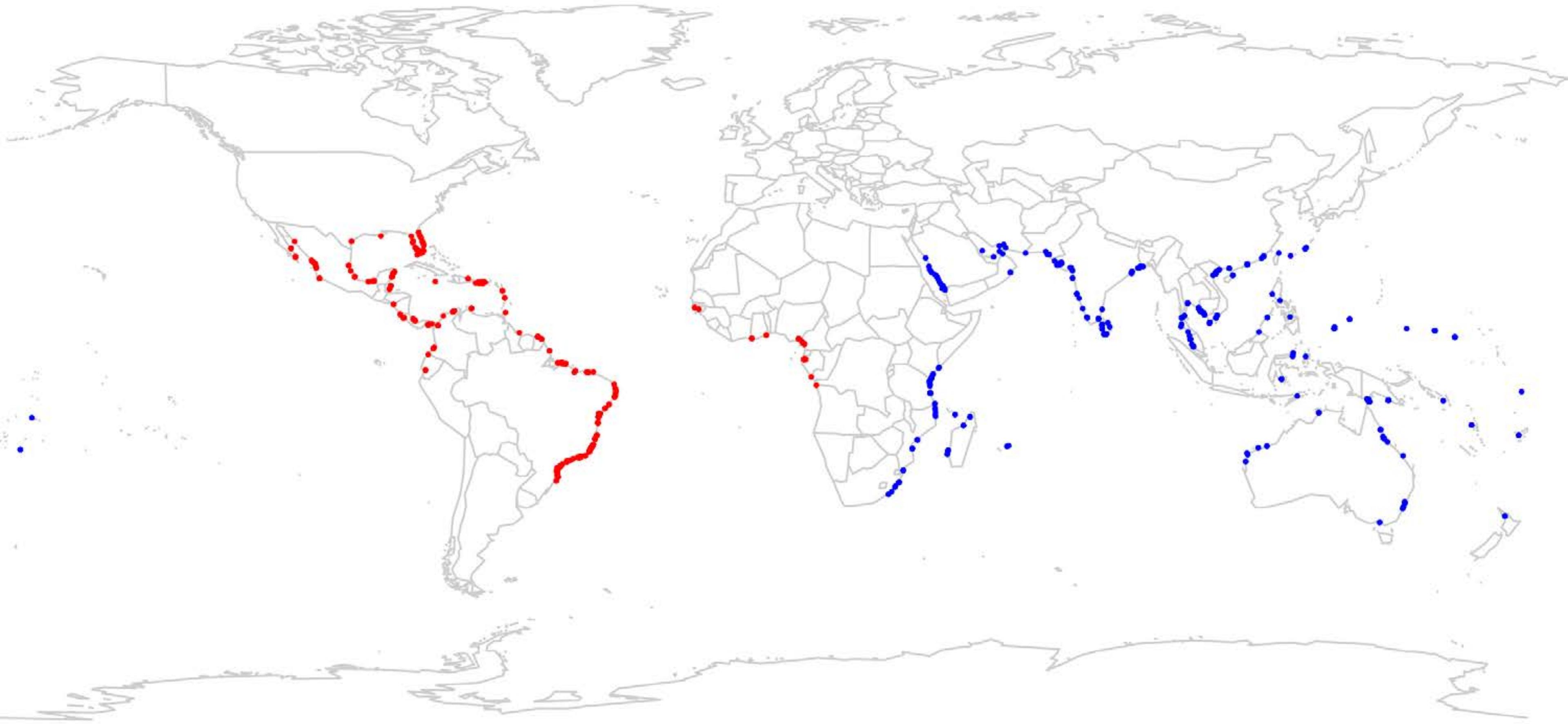
Chisholm & Fung 2021 *Theor. Ecol.*

Mangroves



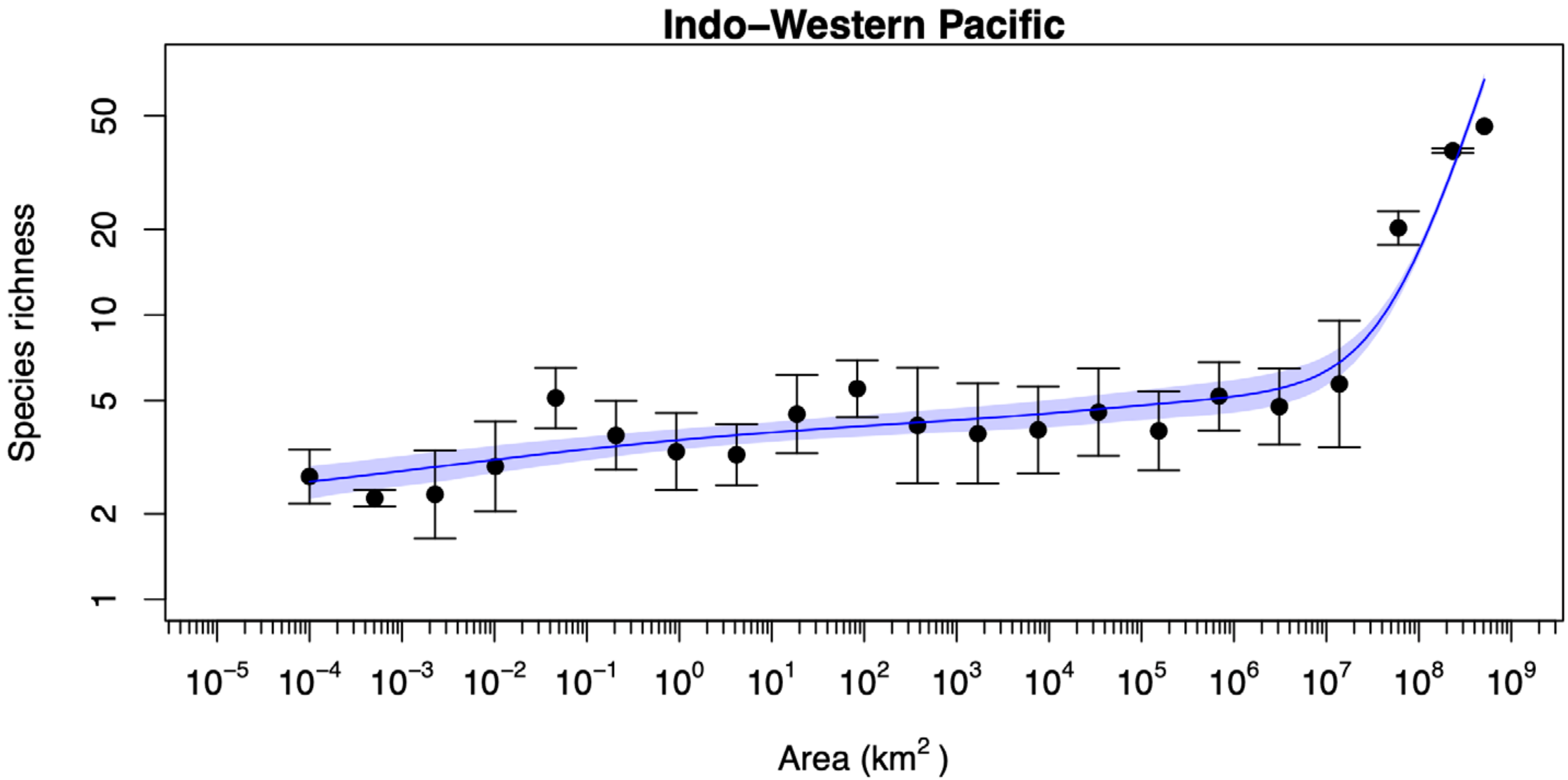
Rull 2022 *Earth. Sci. Rev.*

Mangroves



Chisholm, Fong, Friess & Rovai *Oikos* 2025

Indeed, mangrove tree diversity changes little over nearly ten orders of magnitude of area: a "small-island effect" on the mainland



Chisholm, Fong, Friess & Rovai *Oikos* 2025

Implications

- Novel unified theory predicts communities are niche-assembled under very low immigration, and dispersal-assembled otherwise
- Experimental and observational data suggests niche diversity is usually low (≤10)

⇒ Local communities on mainlands have few niches and are primarily dispersal-assembled

Chisholm & Fung 2021 *Theoretical Ecology*; Loke & Chisholm 2023 *Nature*


Universe Nayr
Distance from origin: 4141.44 km
Latitude: -30.02378°; Longitude: 16.23227°; Altitude: 57.12 m
9414 grouped_objects; 68 species (100.0% new)
Main thread: 4.8 fps
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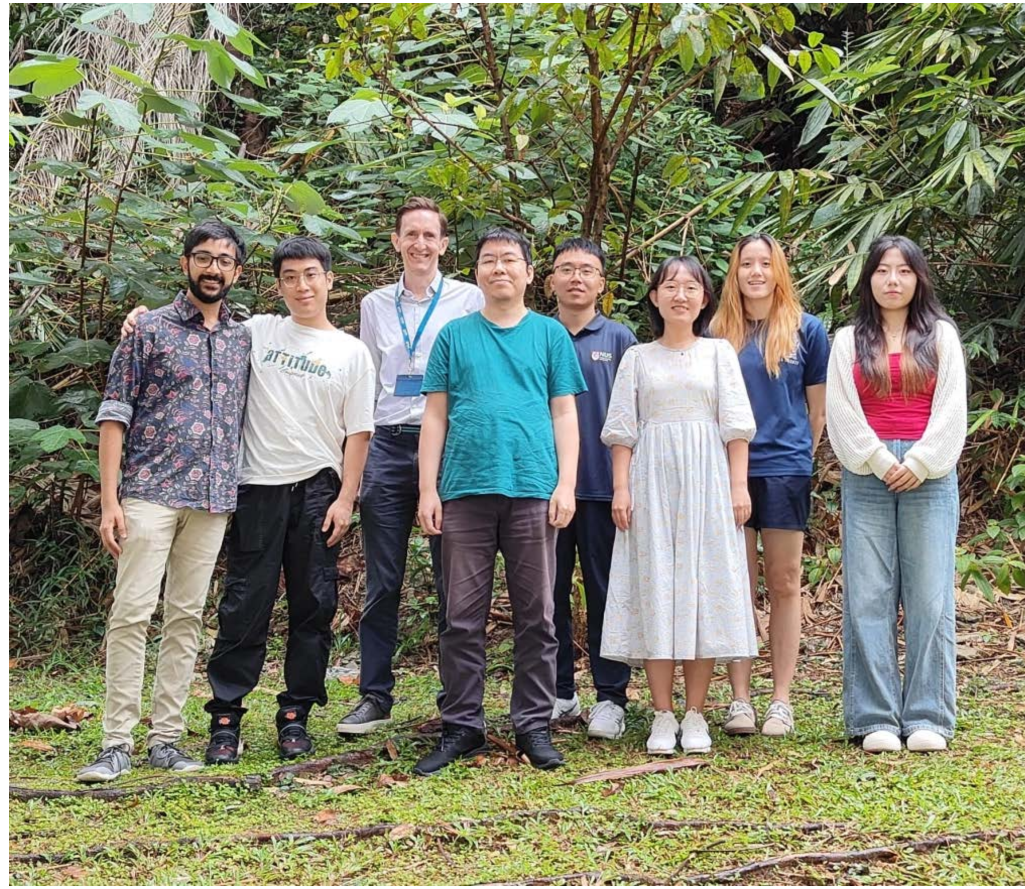

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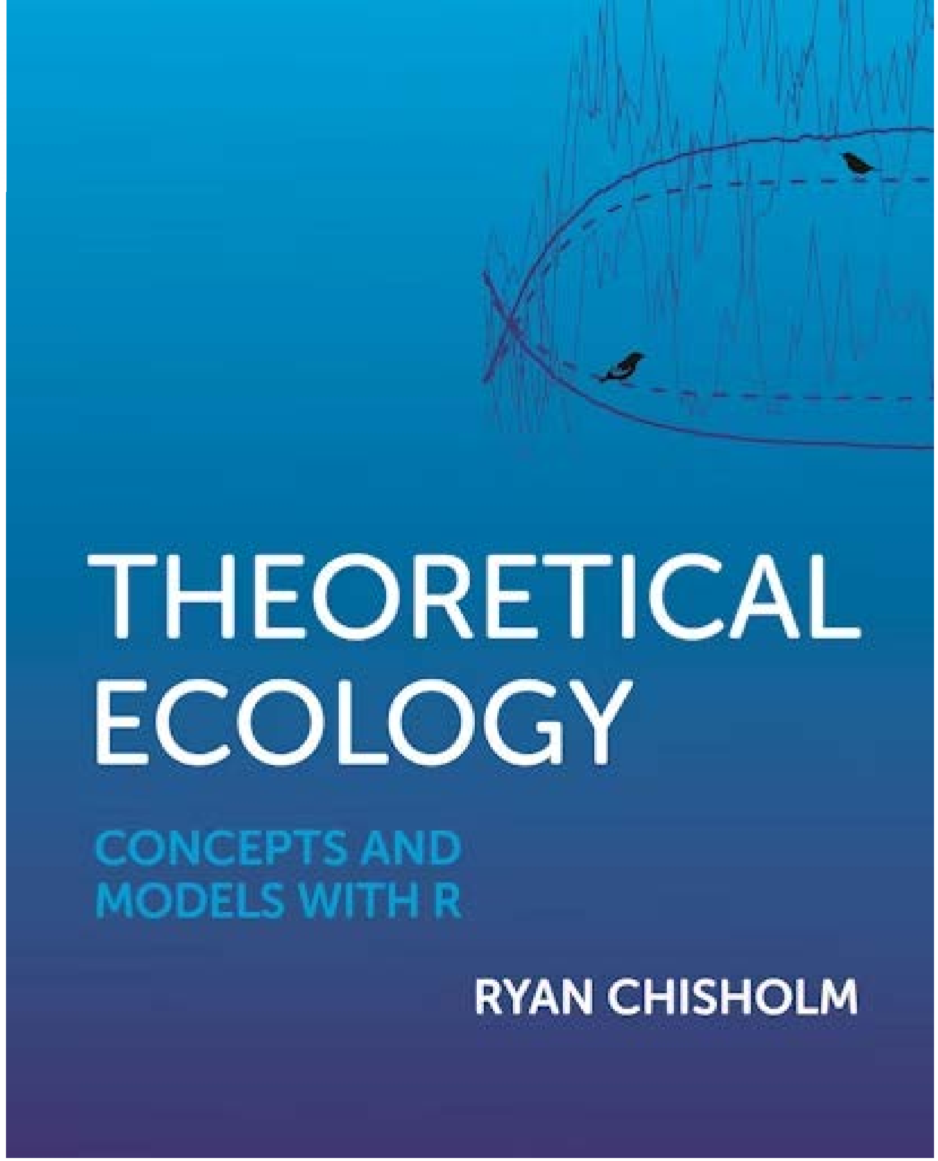

Forthcoming in September 2025