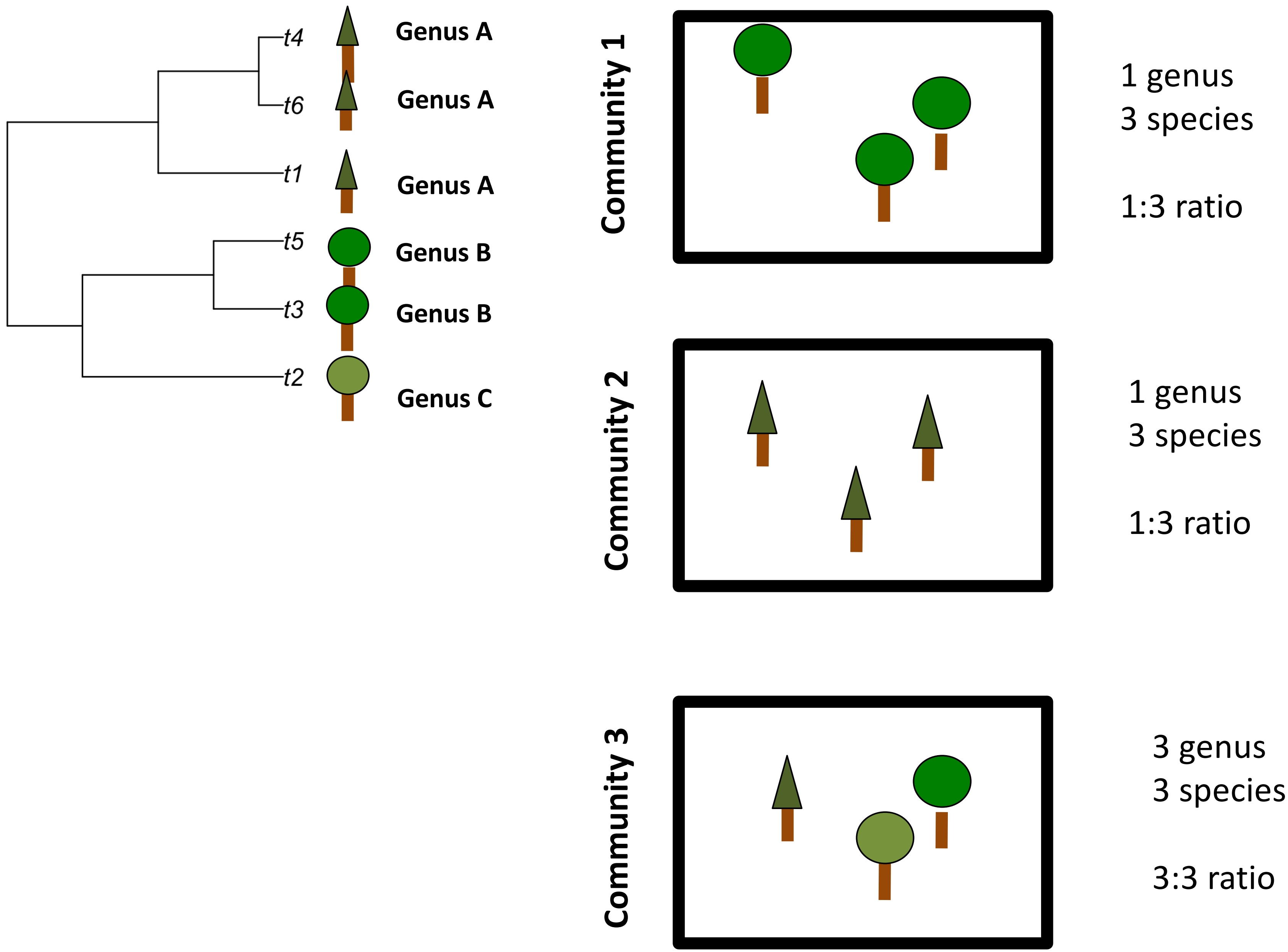
# A Brief History of Null Models

**2 February 2017**
**SESYNC**


t4
Genus A
t6
Genus A
t1
Genus A
t5
Genus B
t3
Genus B
t2
Genus C
Community 1
1 genus
3 species
1:3 ratio
Community 2
1 genus
3 species
1:3 ratio
Community 3
3 genus
3 species
3:3 ratio

# Jarvinen 1982

- Jarvinen, Olli. "Species-to-genus ratios in biogeography: a historical note." *Journal of Biogeography* (1982): 363-370.

# Jarvinen 1982

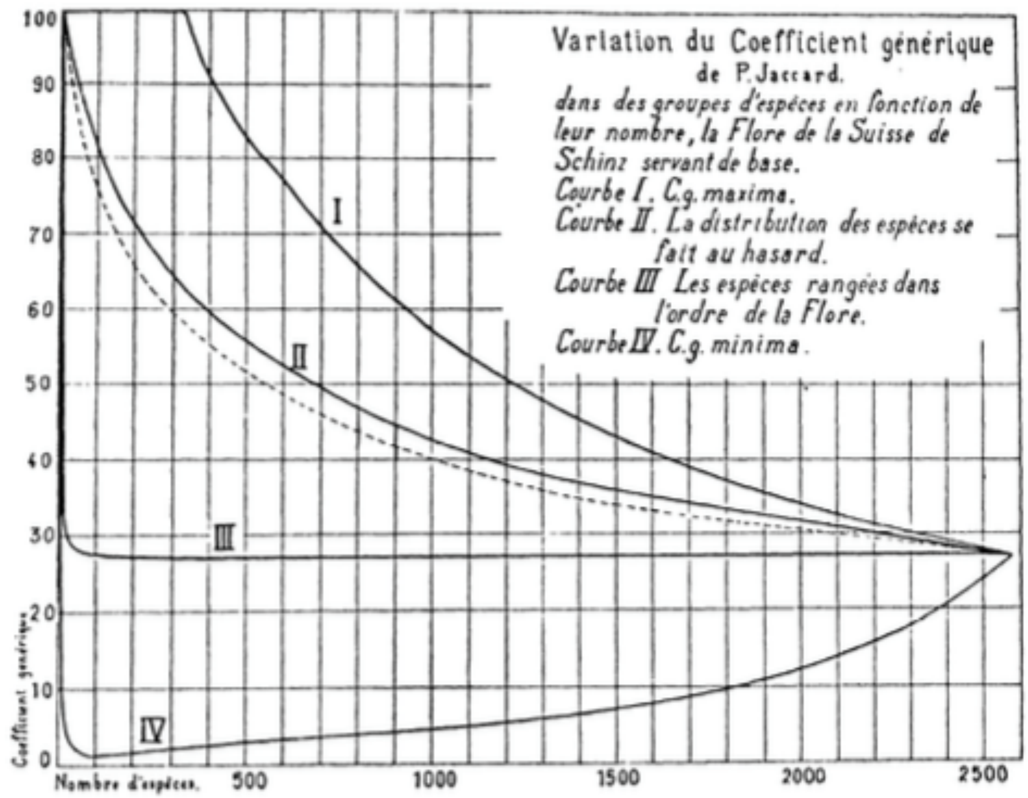
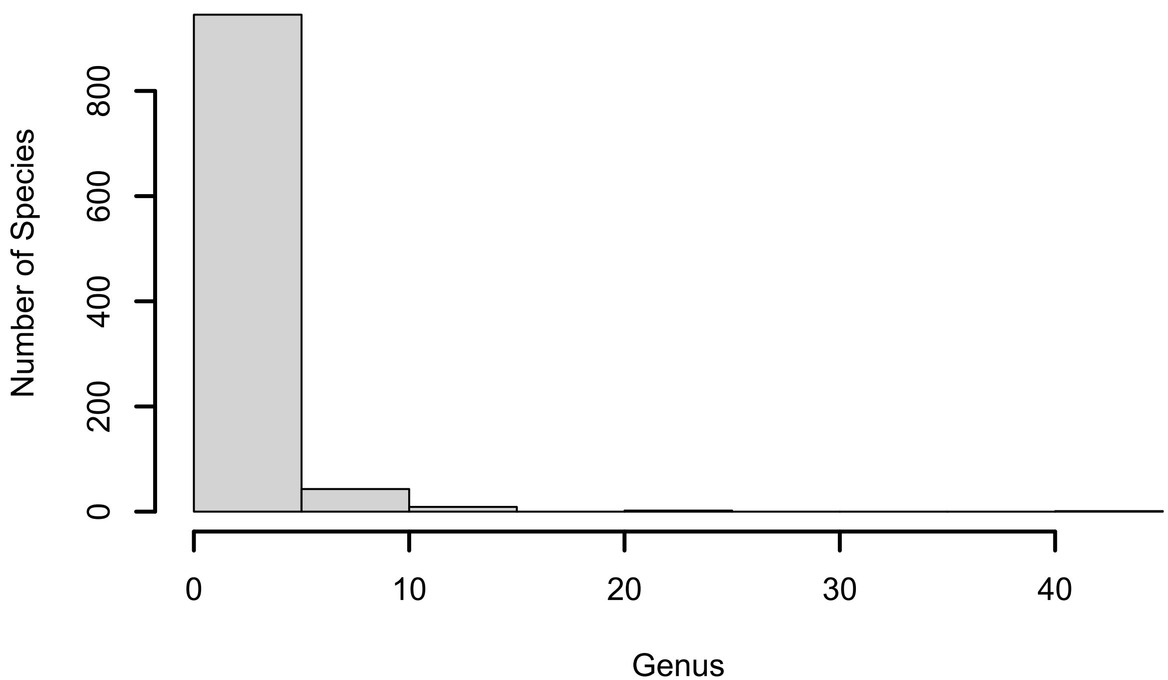
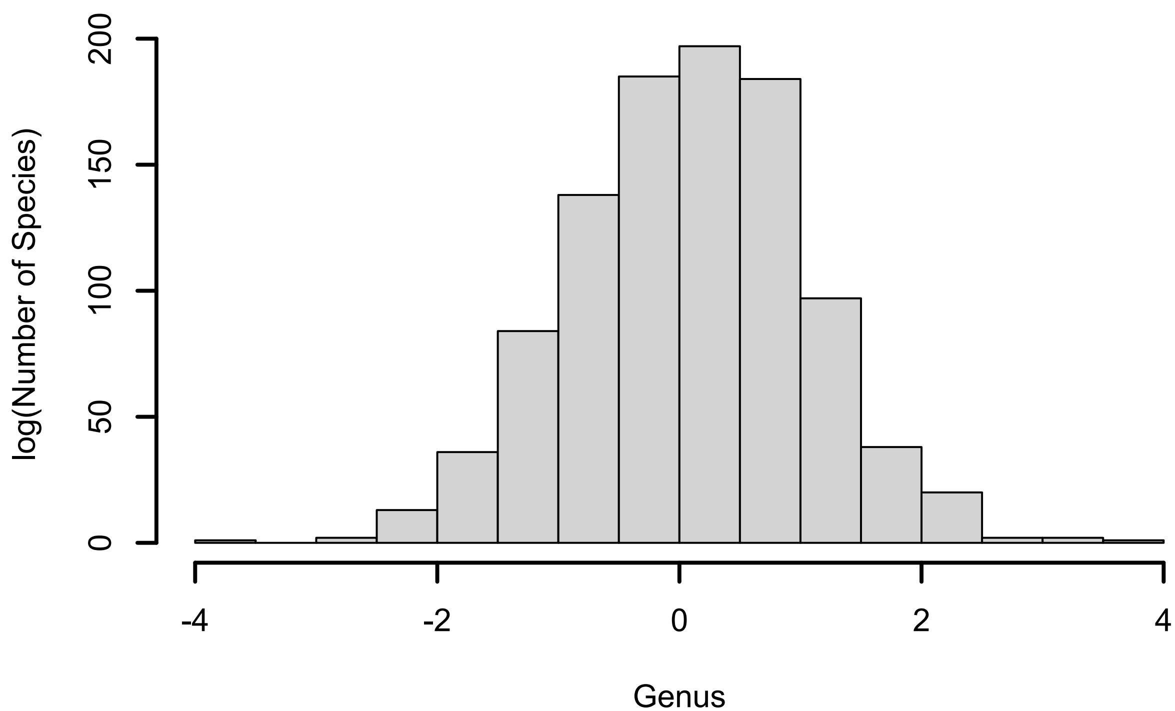



FIG. 1. Maillefer's simulation results showing (I) the maximum and (IV) the minimum values of the G/S ratio (multiplied by 100) in relation to the number of species. Curve II shows the expected value based on sampling without replacement (dashed line shows the standard deviation), and curve III is based on sampling species in the systematic order (standard deviation not given, but it is very large for small S). From Maillefer (1929).

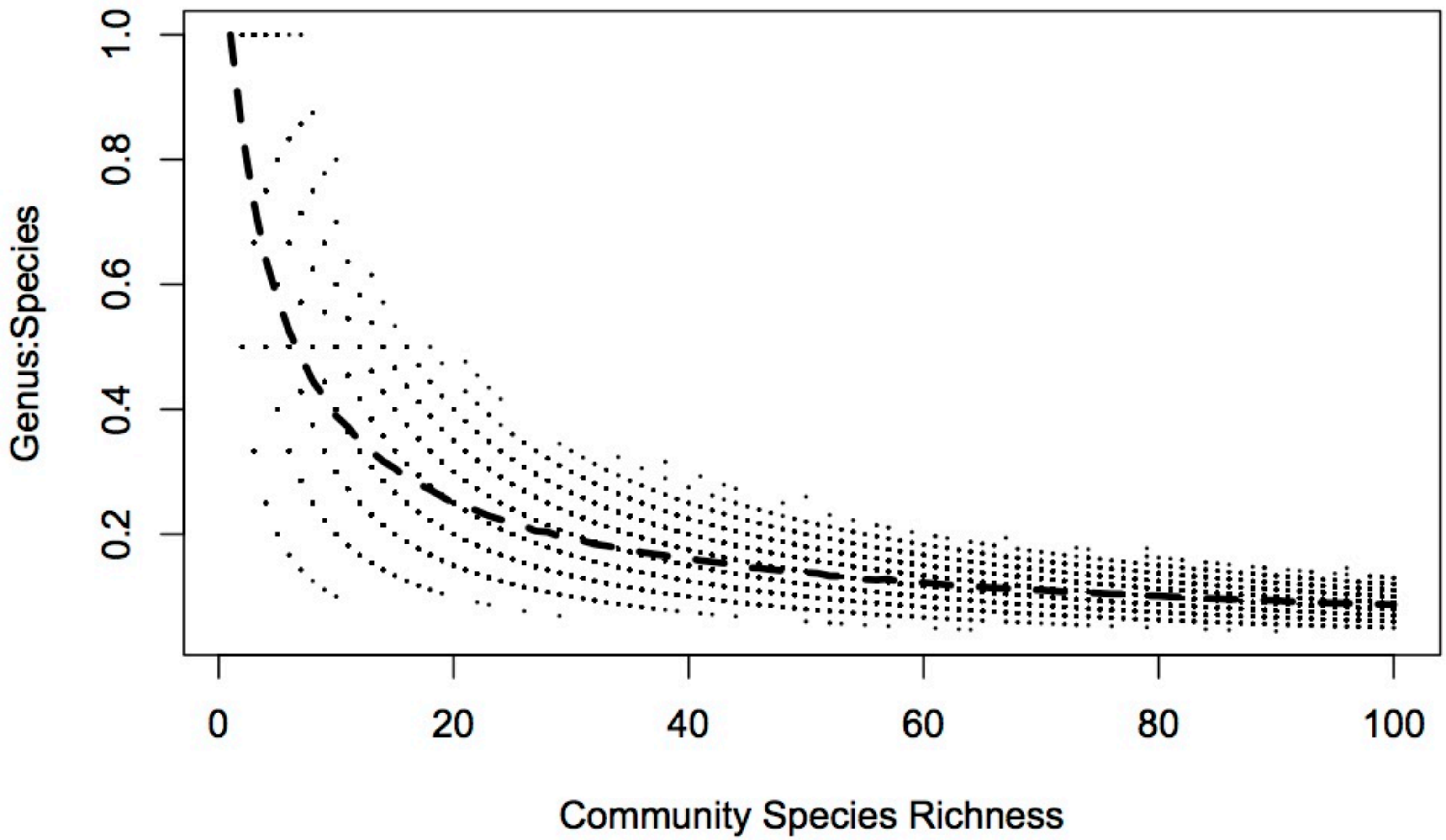
# Simulation



# Simulation

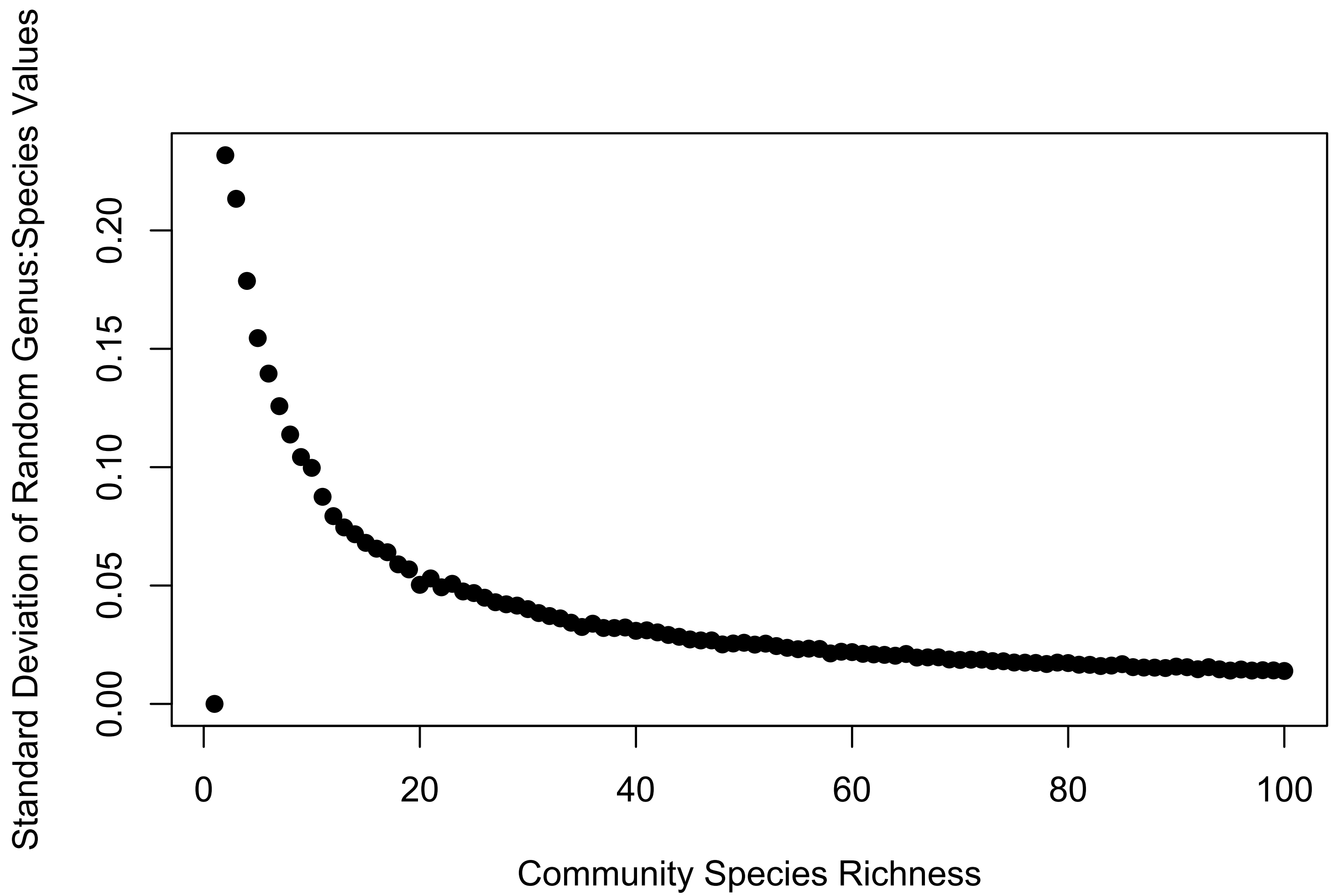


# Simulation



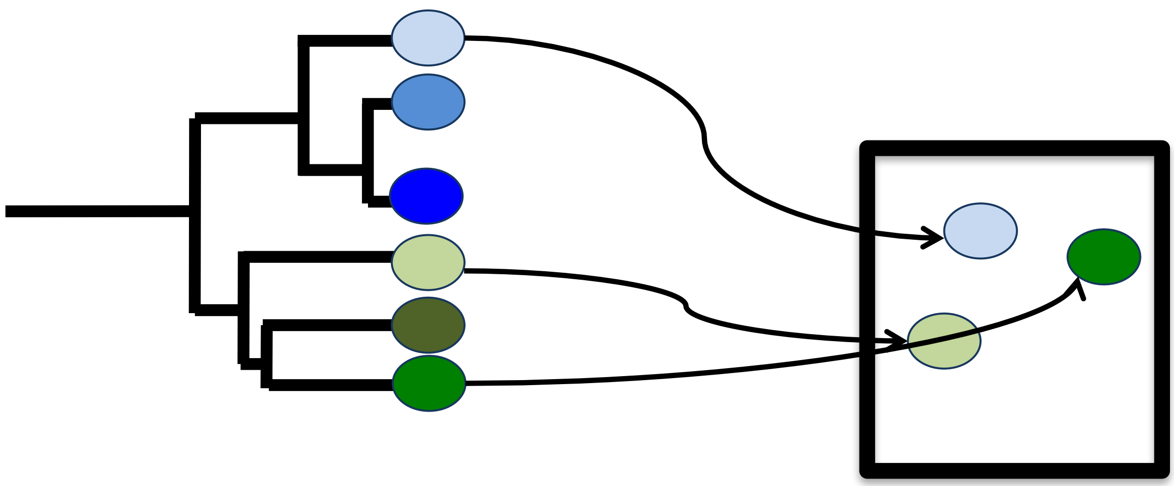
Genus:Species
1.0
0.8
0.6
0.4
0.2
0
20
40
60
80
100
Community Species Richness

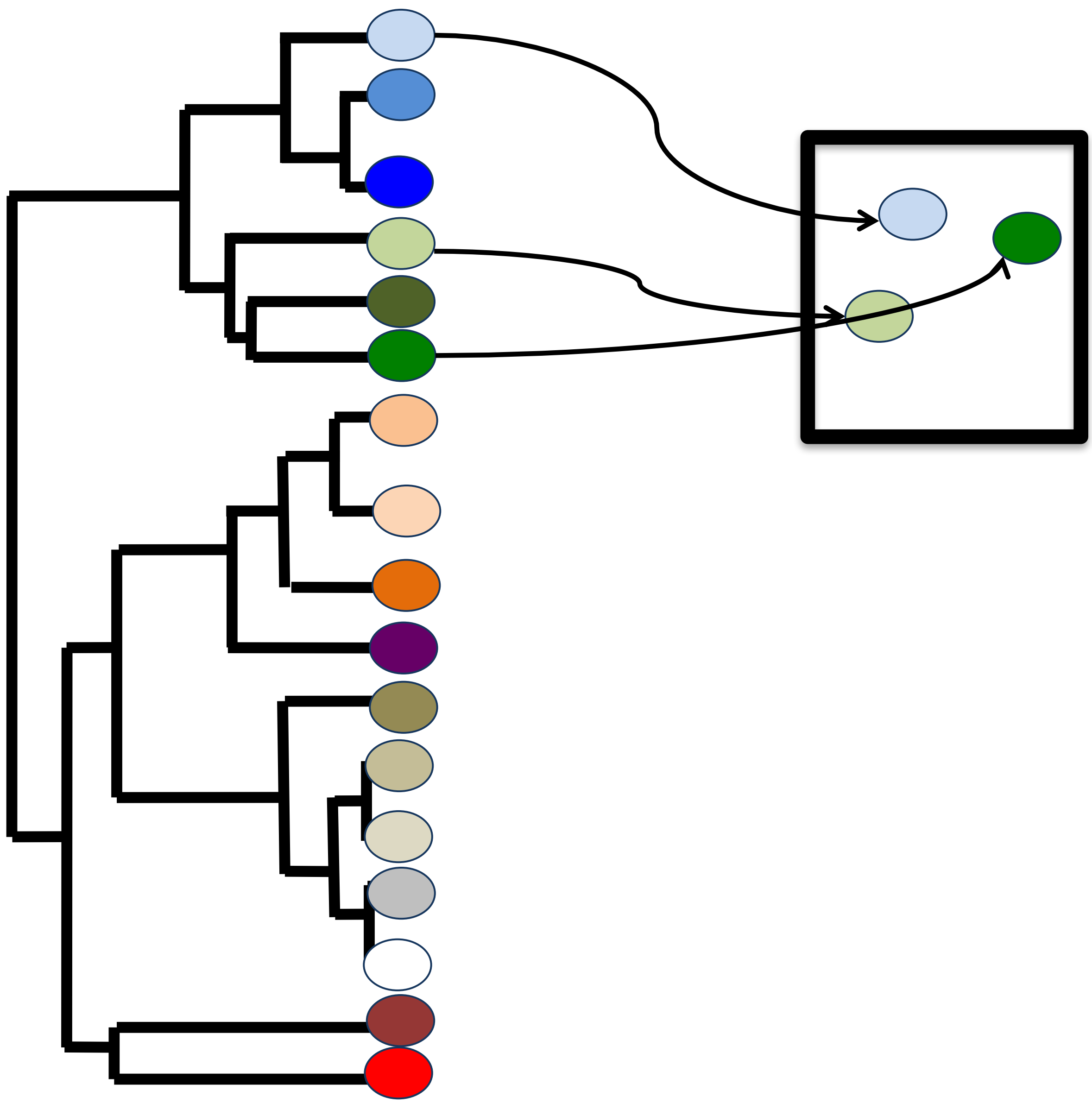
# Simulation


Standard Deviation of Random Genus:Species Values
0.00
0.05
0.10
0.15
0.20
0
20
40
60
80
100
Community Species Richness

# Species Pools

- Null models will require a pool of species to randomly sample
- The output of your analyses could be very sensitive to your decision regarding how species pool definition





# Species Pools

- So how might we define a species pool?

- Is there a species pool?

# Colwell & Winkler 1984

- Colwell, R. K., and D. W. Winkler. "A null model for null models in biogeography." *Ecological communities: conceptual issues and the evidence* 440 (1984): 344-59.

# Colwell & Winkler 1984

- The Narcissus Effect:
  - "Sampling from a post-competition pool under-estimates the role of competition, since its effect is already reflected in the pool"
  - Pool is too small

# Colwell & Winkler 1984

- The Icarus Effect:
  - "Correlations between vagility and morphology can obscure the effects of competition in morphological comparisons of mainland and island biotas"
  - Pool scale as it relates to non-random dispersal ability
    - Pool possibly too inclusive

# Colwell & Winkler 1984

- The J.P. Morgan Effect:
  - "The weaker the taxonomic constraints on sampling, the harder it becomes to detect competition"
  - Pool taxonomic scale

# Grant & Abbott 1980

- Grant, P. R., and I. Abbott. "Interspecific competition, island biogeography and null hypotheses." *Evolution* (1980): 332-341.

# Grant & Abbott 1980

- **“1. The first problem is that the choice of species within families is unfortunate. Species of birds in different genera are less likely to be in the same feeding group or guild than are species in the same genus, and hence are less likely in general to be in potential competition for food …”**

# Grant & Abbott 1980

- **“2. The second problem is in the choice of a mainland area for comparison with the island (Grant, 1966). Geographical variation in community membership and beak sizes of the members within the mainland region could influence the results of a random simulation of the process of island colonization. ”**

# Grant & Abbott 1980

- **“3. In the original analyses Simberloff (1970) assumed equiprobability of dispersal among all species in the mainland pool, in order to obtain expected species/genus ratios on islands. This assumption seems unlikely to be true (Grant, 1970; Terborgh et al., 1978), as has been recently acknowledged, "Biologically this assumption implies that all species have equal dispersal and persistence abilities. In fact, species have different abilities to disperse and persist, and this assumption is therefore absurd" (Connor and Simberloff, 1978).”**

# Keddy & Weiher 1995

- Weiher, Evan, and Paul A. Keddy. "Assembly rules, null models, and trait dispersion: new questions from old patterns." *Oikos* (1995): 159-164.

# Keddy & Weiher 1995

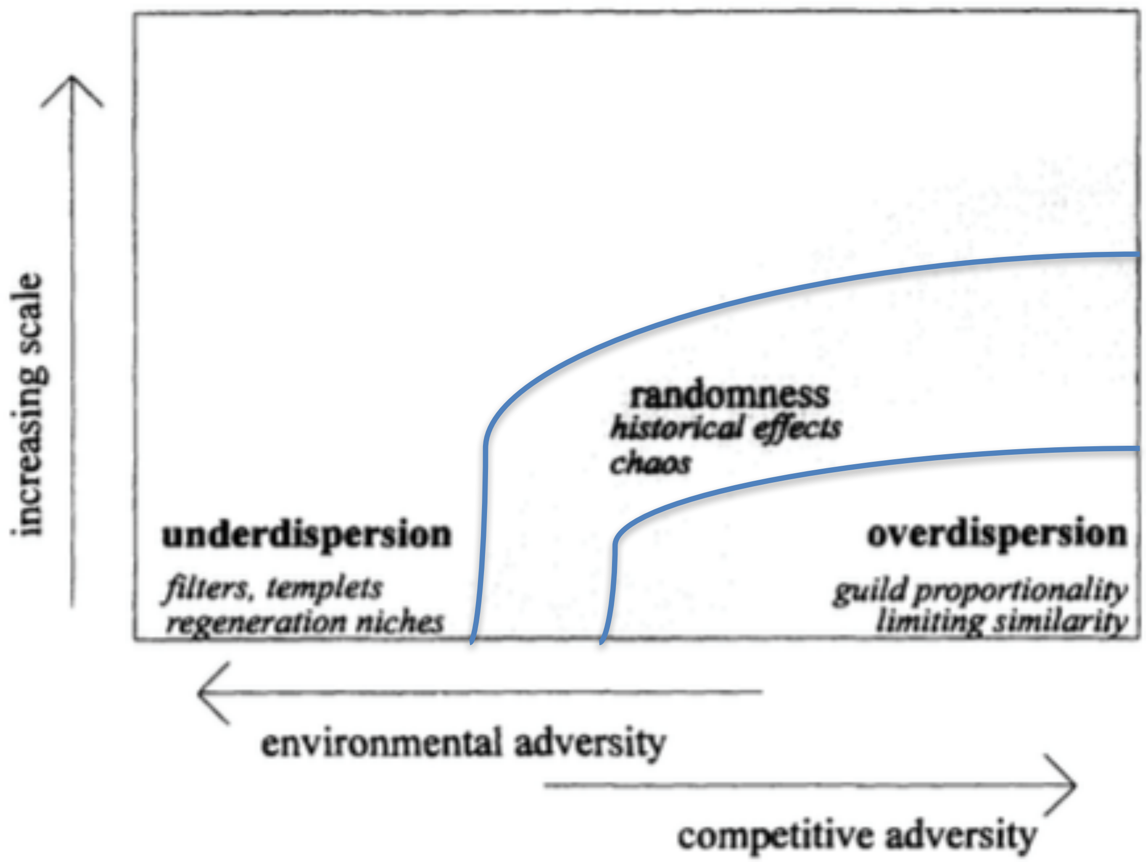



Fig. 1. A qualitative model for trait dispersion.

# Swenson et al. 2006 Ecology

*Ecology*, 87(10), 2006, pp. 2418–2424
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## THE PROBLEM AND PROMISE OF SCALE DEPENDENCY IN COMMUNITY PHYLOGENETICS

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[2]*Institute for Tropical Ecosystems Research, University of Puerto Rico, Rio Piedras, Puerto Rico 00931 USA*

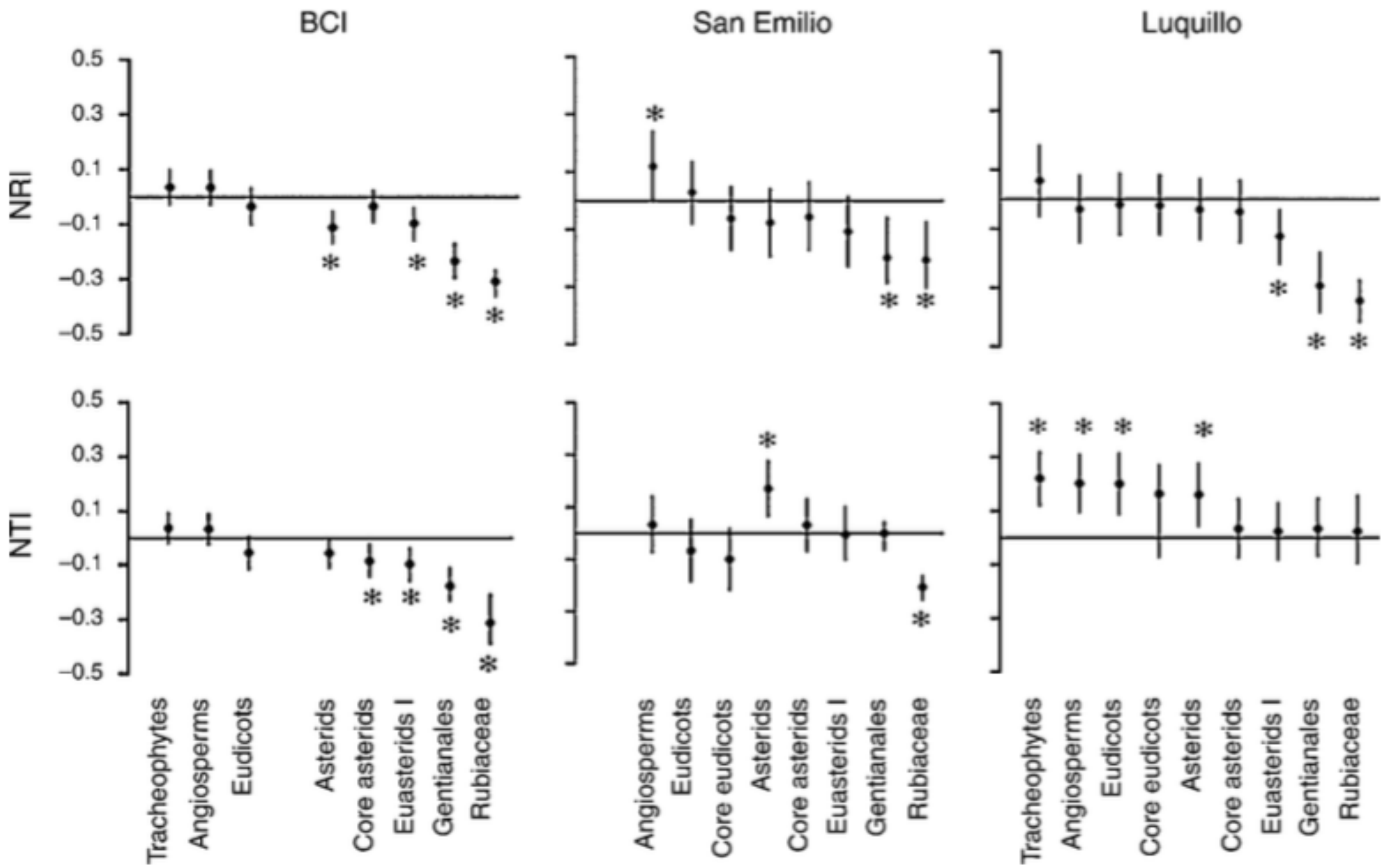
# Swenson et al. 2006 Ecology

TABLE 1. The number of species in pools ($n$) at each scale utilized and the forest types included in the pool.

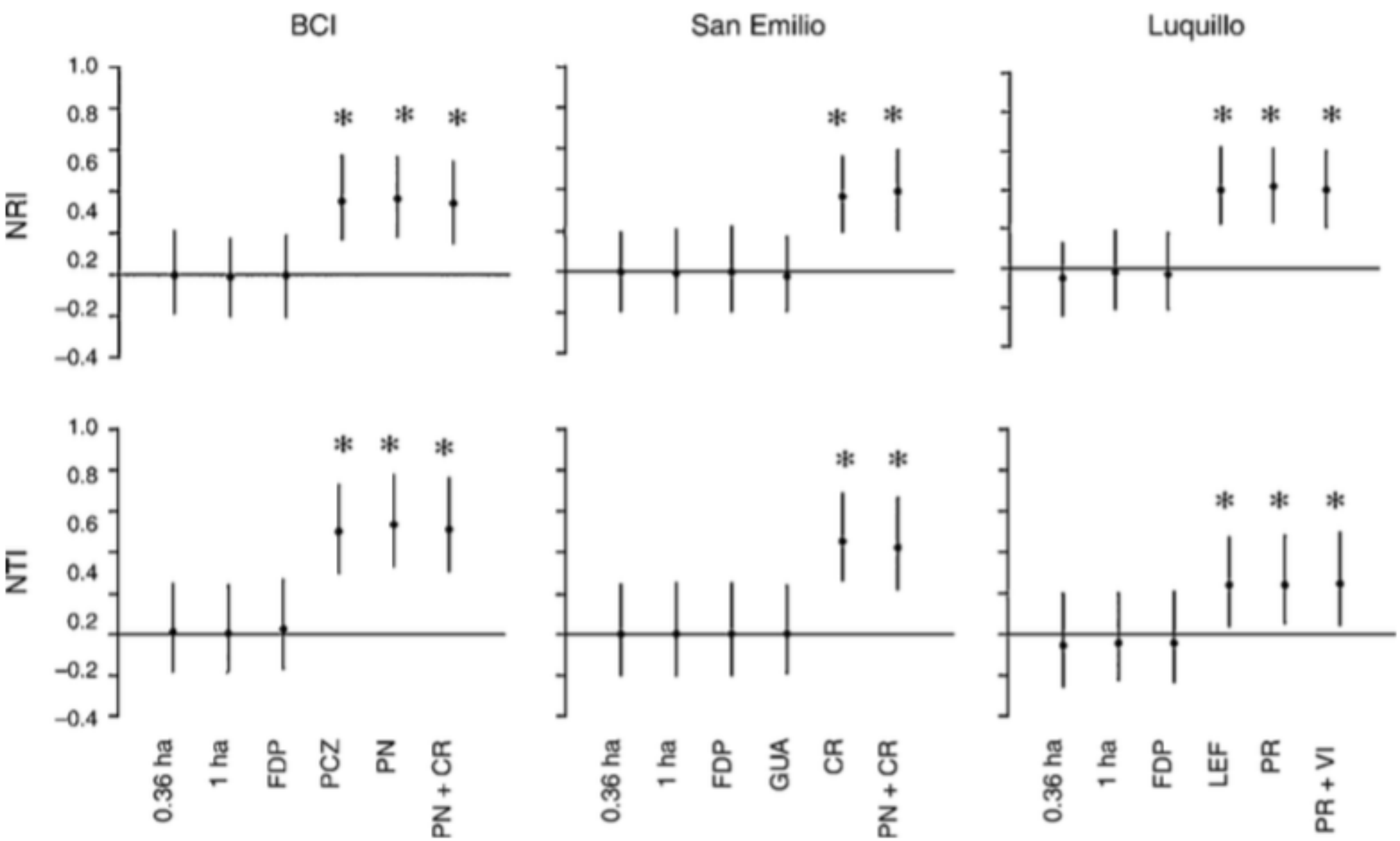
| | 0.36 ha | | 1 ha | | FDP | | Region | | Country | | Multiple countries | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Location | $n$ | Forest types | $n$ | Forest types | $n$ | Forest types | $n$ | Forest types | $n$ | Forest types | $n$ | Forest types |
| BCI† | 118–144 | moist | 157–181 | moist | 301 | moist | 1270 | dry, moist, wet forests | 2446 | cloud, dry, moist, wet forests | 3435 | cloud, dry, moist, wet forests |
| San Emilio | 55–74 | dry | 85–88 | dry | 173 | dry | 197 | dry forest | 2261 | cloud, dry, moist, wet forests | 3435 | cloud, dry, moist, wet forests |
| Luquillo | 49–70 | moist | 71–87 | moist | 151 | moist | 281 | cloud, moist, wet forests | 738 | cloud, dry, moist, wet forests | 779 | cloud, dry, moist, wet forests |

† Barro Colorado Island.

# Swenson et al. 2006 Ecology



# Swenson et al. 2006 Ecology



# Swenson et al. 2007 Ecology

*Ecology*, 88(7), 2007, pp. 1770–1780
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## THE INFLUENCE OF SPATIAL AND SIZE SCALE ON PHYLOGENETIC RELATEDNESS IN TROPICAL FOREST COMMUNITIES

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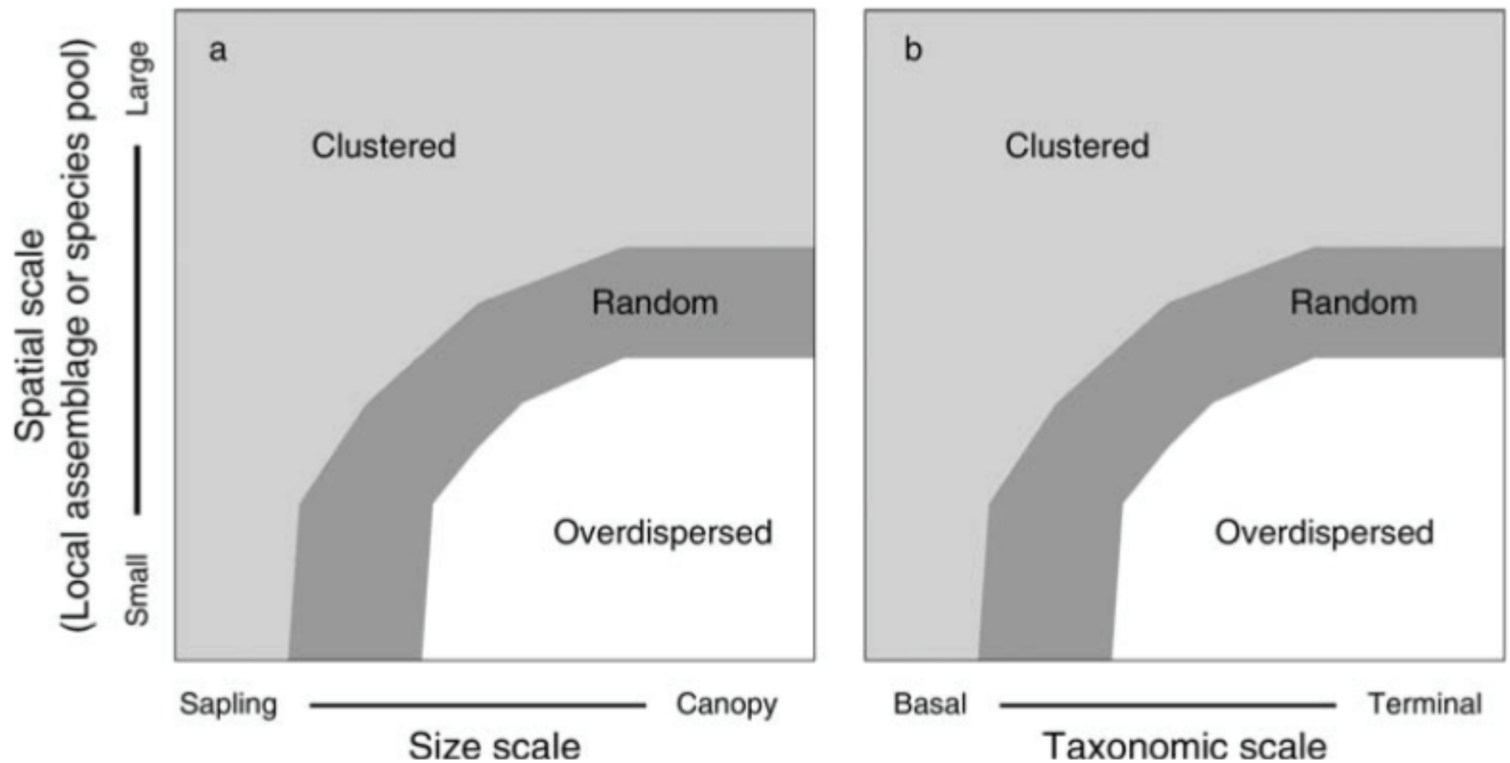


FIG. 4. (a) A figure adapted from Weiher and Keddy (1995), depicting a graphical model of the effect of spatial and body size scale on phylogenetic dispersion in ecological communities. (b) A graphical model of the spatial and taxonomic scale dependency of phylogenetic dispersion in ecological communities. The graphical predictions presented are based on and consistent with the findings of this study and Swenson et al. (2006).

*Ecology*, 87(7) Supplement, 2006, pp. S86–S99
© 2006 by the Ecological Society of America

# THE PHYLOGENETIC STRUCTURE OF A NEOTROPICAL FOREST TREE COMMUNITY

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[2]*Department of Plant Biology, University of Georgia, Athens, Georgia 30602 USA*

TABLE 2. Tree community phylogenetic structure in quadrats at four spatial scales within the 50-ha Forest Dynamics Plot on Barro Colorado Island, Panama.

| | | Net relatedness index | | | Nearest taxon index | | |
|---|---|---|---|---|---|---|---|
| Spatial scale | $N$ | Estimated mean | SE | $P$ | Estimated mean | SE | $P$ |
| Unconstrained null model | | | | | | | |
| 10 × 10 m | 5000 | 0.260 | 0.008 | 0.0001 | 0.142 | 0.012 | 0.0001 |
| 20 × 20 m | 1250 | 0.389 | 0.016 | 0.0001 | 0.154 | 0.021 | 0.0001 |
| 50 × 50 m | 200 | 0.771 | 0.047 | 0.0001 | 0.453 | 0.045 | 0.0001 |
| 100 × 100 m | 50 | 0.074 | 0.099 | 0.4605 | −0.019 | 0.099 | 0.8459 |
| Constrained null model | | | | | | | |
| 10 × 10 m | 5000 | 0.061 | 0.016 | 0.0001 | 0.070 | 0.014 | 0.0001 |
| 20 × 20 m | 1250 | 0.056 | 0.033 | 0.0952 | 0.020 | 0.028 | 0.4854 |
| 50 × 50 m | 200 | 0.051 | 0.093 | 0.5825 | −0.046 | 0.076 | 0.5427 |
| 100 × 100 m | 50 | 0.043 | 0.180 | 0.8110 | 0.003 | 0.161 | 0.9858 |

*Notes:* Net relatedness index (NRI) and nearest taxon index (NTI) are measures of community phylogenetic structure based on constrained and unconstrained null models (see *Methods* for description). Positive NRI and NTI values indicate phylogenetic clustering; negative values indicate phylogenetic overdispersion of species occurring together in a quadrat. Parameter estimates at each scale are based on a spatial generalized least-squares model with a first-order spatial-neighbor simultaneous spatial autoregression term (SAR). Significant $P$ values indicate that the phylogenetic structure at a given spatial scale differed from zero according to a two-tailed $t$ test.

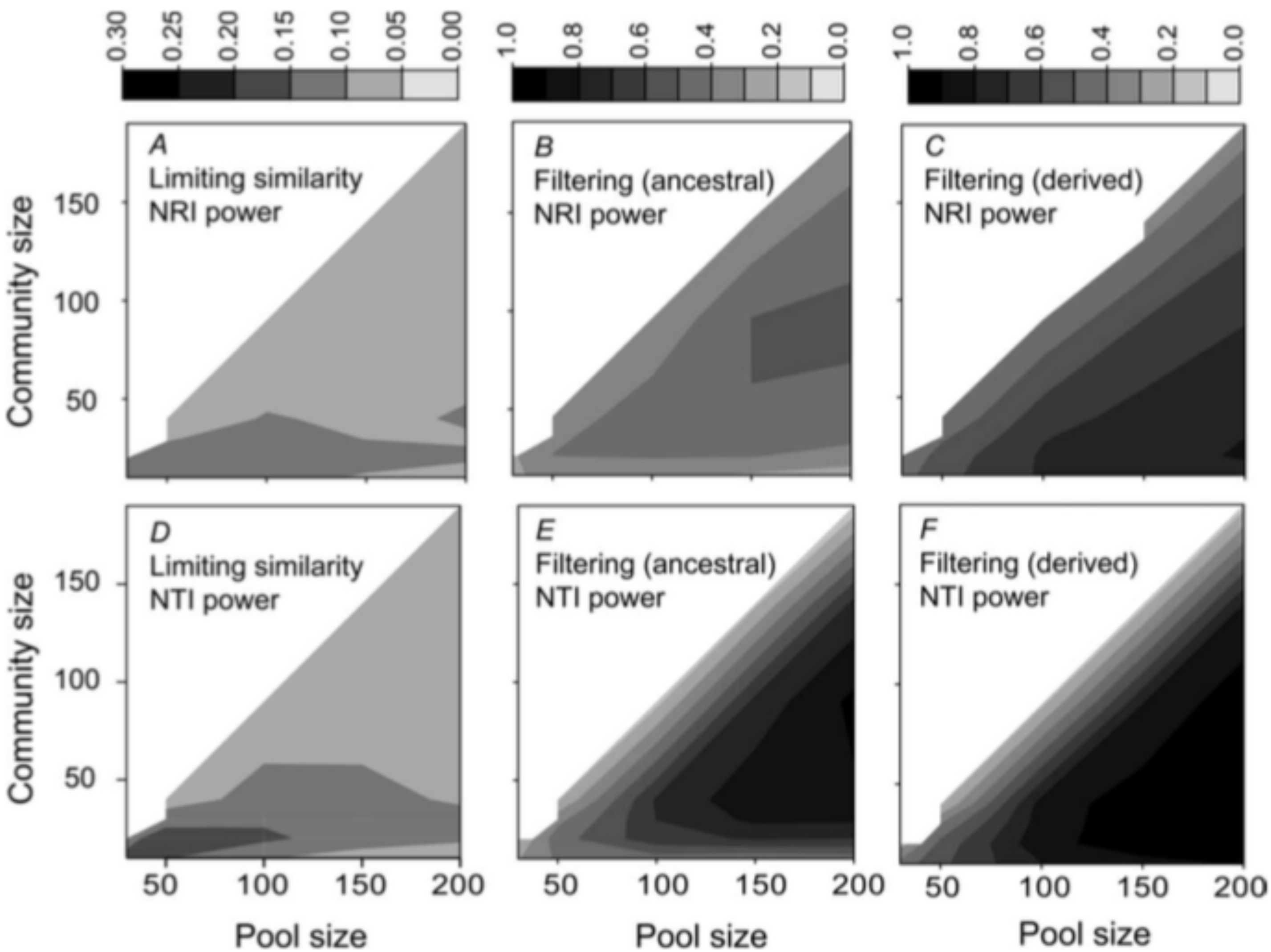
# Kraft et al. 2007

VOL. 170, NO. 2 THE AMERICAN NATURALIST AUGUST 2007

## Trait Evolution, Community Assembly, and the Phylogenetic Structure of Ecological Communities

Nathan J. B. Kraft,[1,*] William K. Cornwell,[2,†] Campbell O. Webb,[3,‡] and David D. Ackerly[1,§]

# Kraft et al. 2007



# Kraft & Ackerly 2010

*Ecological Monographs*, 80(3), 2010, pp. 401–422
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## Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest

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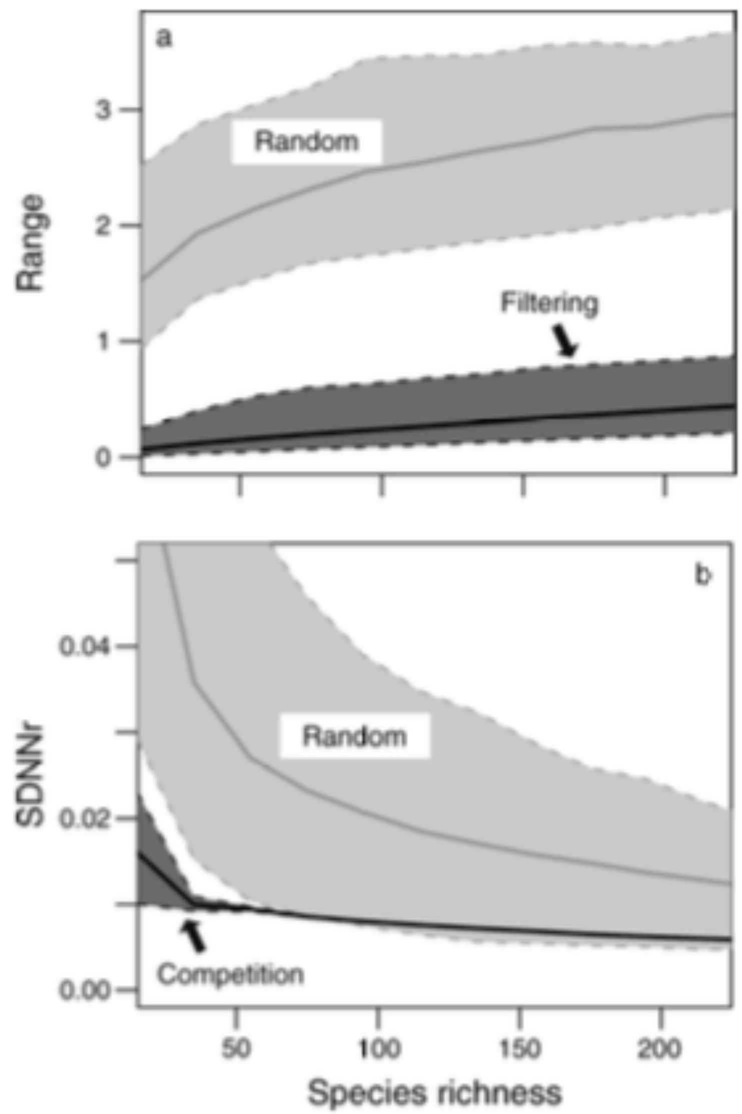
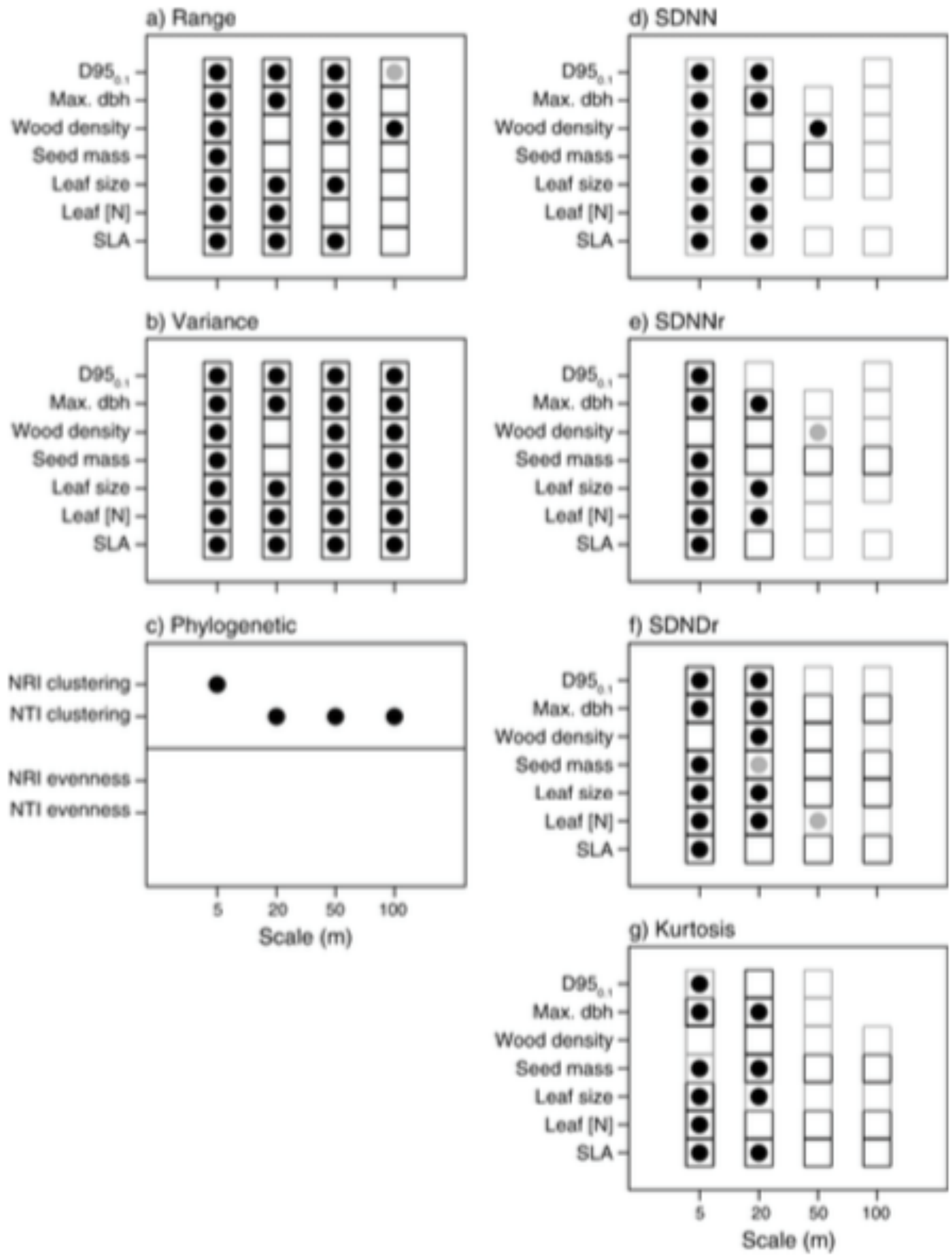


a
Range
3
2
1
0
Random
Filtering
b
SDNNr
0.04
0.02
0.00
Random
Competition
50
100
150
200
Species richness


a) Range
b) Variance
c) Phylogenetic
d) SDNN
e) SDNNr
f) SDNDr
g) Kurtosis
D95$_{0.1}$
Max. dbh
Wood density
Seed mass
Leaf size
Leaf [N]
SLA
NRI clustering
NTI clustering
NRI evenness
NTI evenness
5
20
50
100
Scale (m)