Environment vs. species input controls of diversity

Modeling diversity and distributions in tree communities

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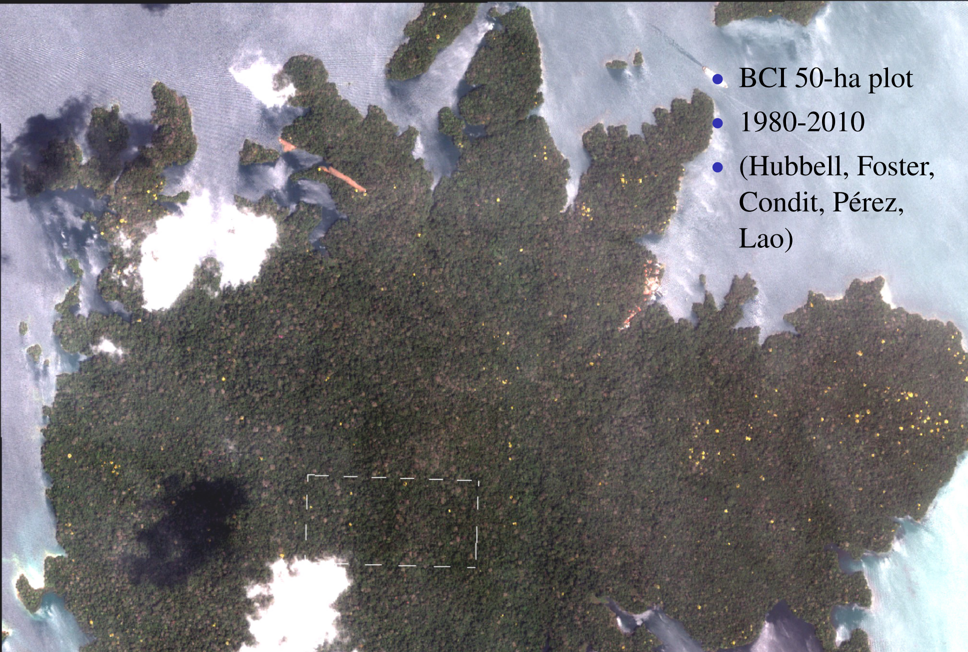
- Why are there so few species in the north?
- Do 1100 species in a small area have their own niches?
  - Soil moisture niches?
  - Herbivore niches?
- Are 1100 species in a small area demographically identical (the neutral theory)?

Outline

CTFS forest census plots



- BCI 50-ha plot
- 1980-2010
- (Hubbell, Foster, Condit, Pérez, Lao)

Conclusions: my view of forest diversity

- No local stabilizing forces sufficient to maintain observed diversity
- Diversity at 50 ha maintained by species input

Conclusions: my view of forest diversity

- Dispersal effective over 10s to 100 km
- Most species locally are demographically neutral, or even sinks

Conclusions: my view of forest diversity

- At the wider scale, hundreds of run-of-the-mill environmental niches are easy to understand

Importance of the neutral theory

- is not neutrality

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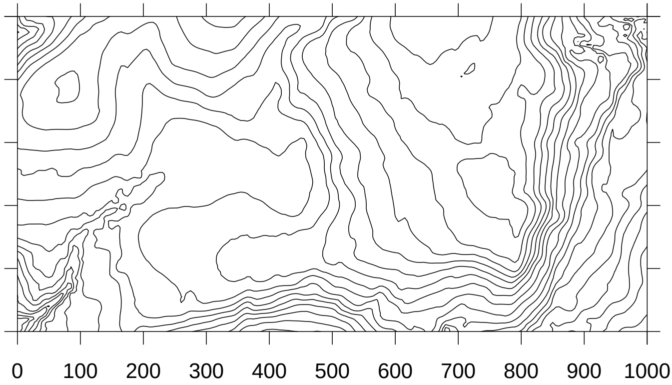
- it's the focus on speciation and species input as cause of diversity
- and on stochastic populations of individuals

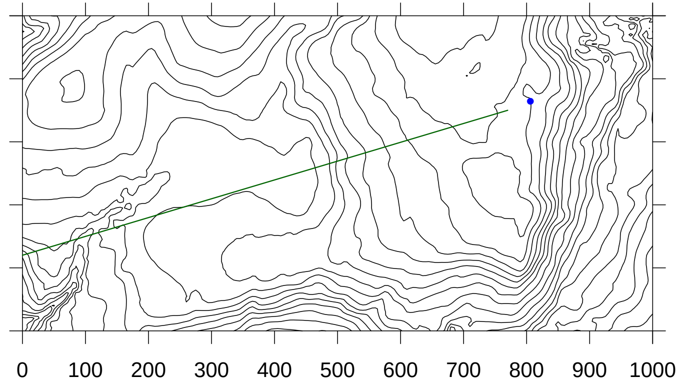
Rauvolfia littoralis
in 1990



Observing species input

Rauvolfia littoralis in 1995

The species had never been seen anywhere on BCI before



Quantifying species input

Rate of input ν needed to maintain observed diversity is predicted exactly under stochastic dynamics

input predicted:

- BCI

input observed

- BCI 1990-95:

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  - $\nu = \frac{S_1}{J} = \frac{23}{2.3 \times 10^5}$
  - $= 1.0 \times 10^{-4}$

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  - 4 new species among 21727 recruits
  - (*Cecropia longipes, Psychotria psychotriifolia, Rauvolfia littoralis, Vismia macrophylla*)

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  - (*Cecropia longipes, Psychotria psychotriifolia, Rauvolfia littoralis, Vismia macrophylla*)
  - $= 1.8 \times 10^{-4}$

Rate of input ν needed to maintain observed diversity is predicted exactly under stochastic dynamics

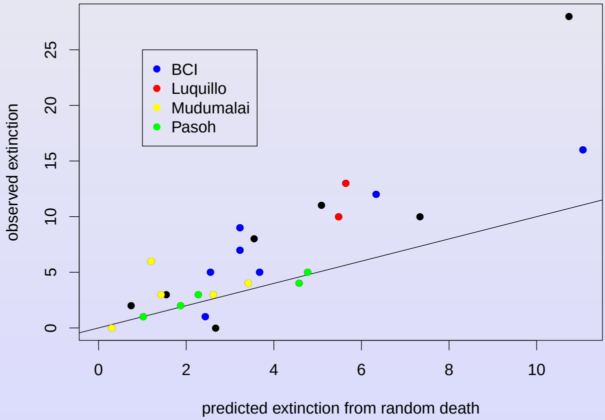
input predicted:

- Luquillo diversity:
  - $= 1.9 \times 10^{-4}$

input observed

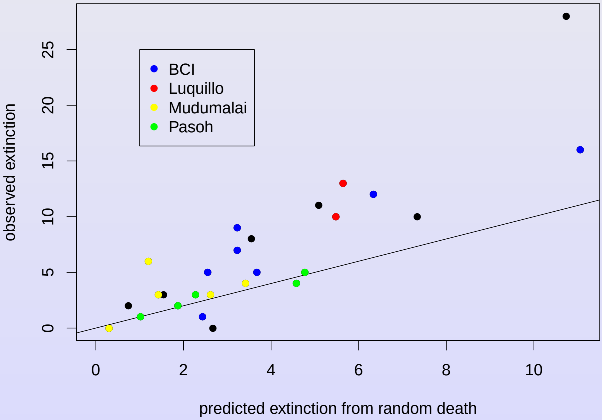
- Luquillo 1996-2001:
  - 5 new species among 25090 recruits
  - (*Mimosa pudilla, Phytolacca rivinoides, Piper pellatata, Neuroleana lobata, Rauvolfia nitida*)
  - $= 2.0 \times 10^{-4}$

Local extinction can be quantified



- it must to balance species input
- observed rates are higher than expected from random death (10 different CTFS plots)

Local extinction can be quantified



- they should be lower under stabilizing dynamics

Species turnover is routine

Take-home message:

Species turnover is observed and maintains diversity
Local stabilizing forces do not maintain diversity

- Several lines of evidence demonstrate
  - Tree species are well-dispersed over 50 ha
  - Seeds and saplings often 100-1000 m from parents
- Important question in dispersal
  - How frequent are 1-10 km and 10-100 km dispersal events?

Cavanillesia platanifolia

Modeling communities of trees

Start with observable traits of individuals:

- Mortality
- Reproduction
- Growth
- Dispersal
- Speciation

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Predicting community patterns:

- Diversity
- Abundance
- Spatial patterns
- Species-area relationship
- Extinction

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Community properties of broad interest emerge from the model without any direct assumptions

Lecointea amazonica

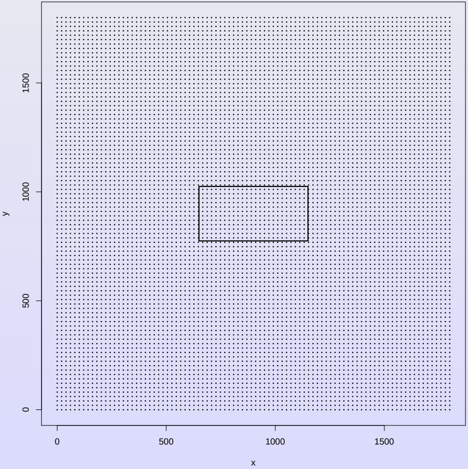
- coexistence theories are not diversity theories

Coexistence vs. diversity models

Lecointea amazonica

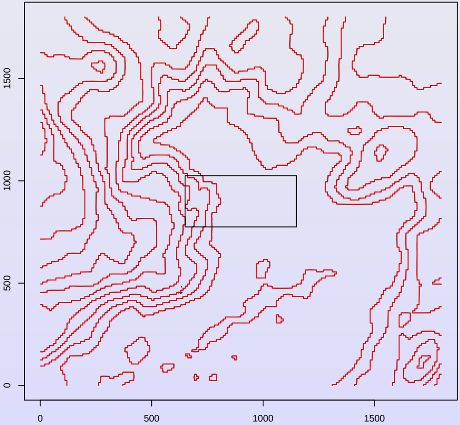
- coexistence theories are not diversity theories
- predicting diversity requires theories of
  - species input
  - extinction
  - population size
  - plus coexistence mechanisms

Fig. 6.1



Hubbell model = voter model

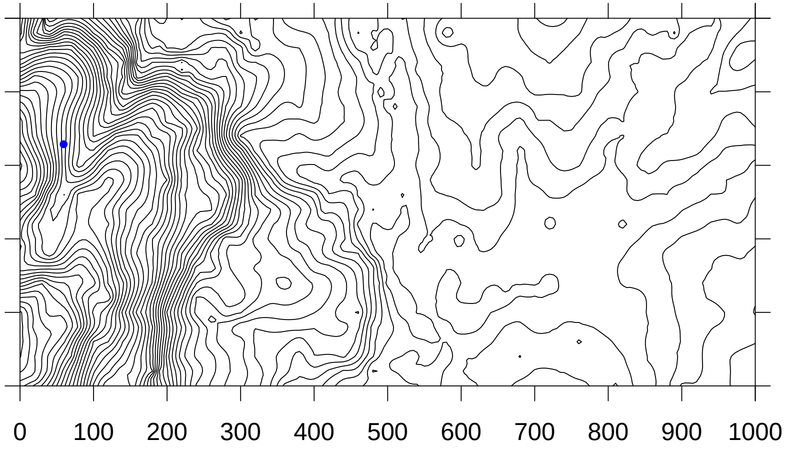
- grid of 1800x1800 trees
- core of 500x250 trees avoids edges



Features added to neutral model:

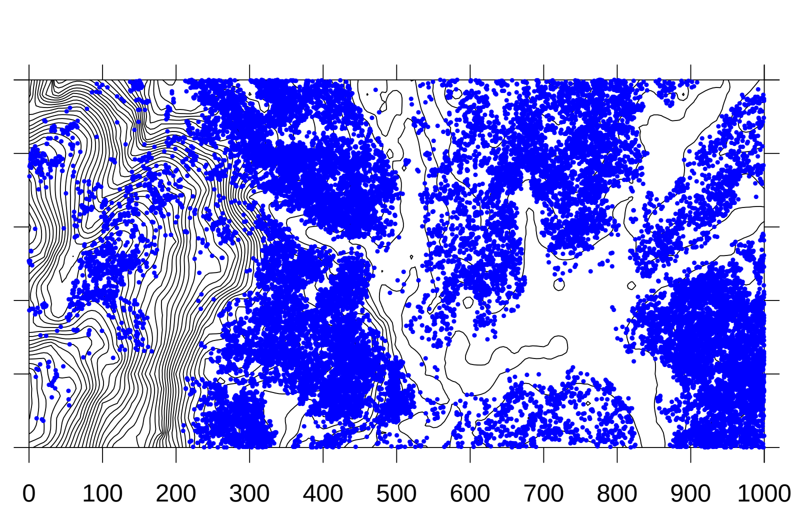
- variation in dispersal distance
- niche differences: mortality varies with topography
- delayed maturation

Manilkara lososiana (Sapotaceae)

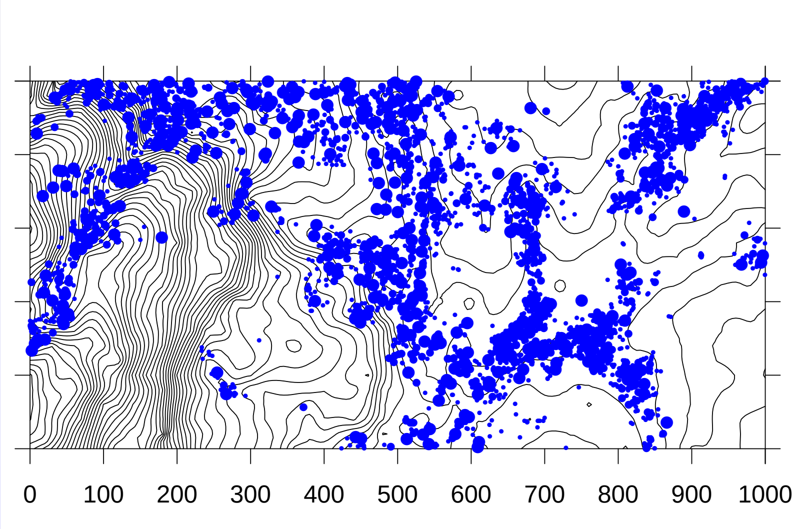


D. Thomas, D. Kenfack, G. Chuyong, R. Condit
492 species & 329,000 individuals

Cola semecarpophylla (Malvaceae)



Protomegabaria stipitata (Euphorbiaceae)



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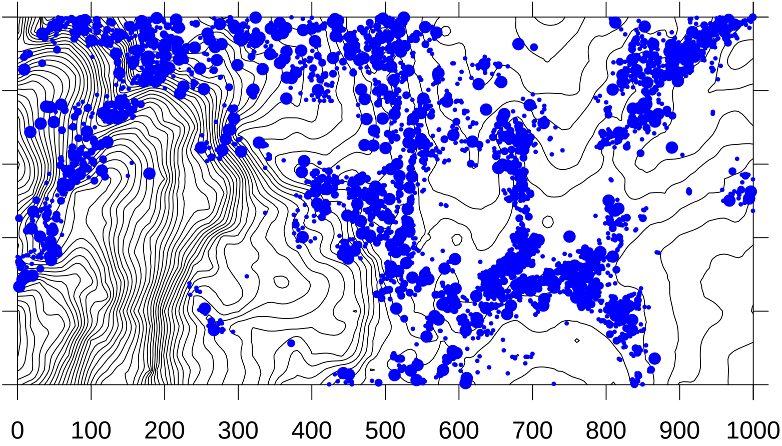
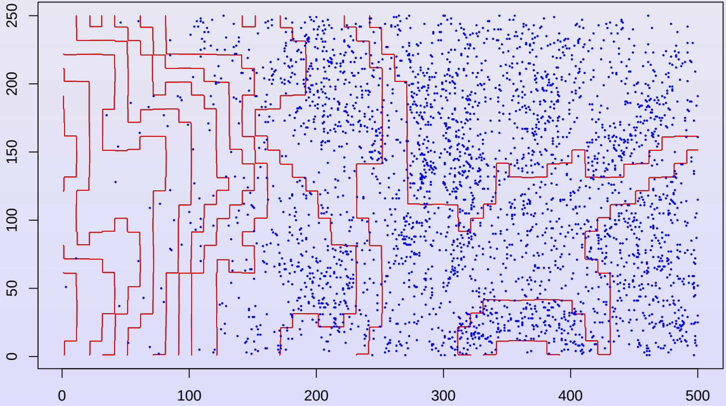


Species 108 has high survival in low non-depression



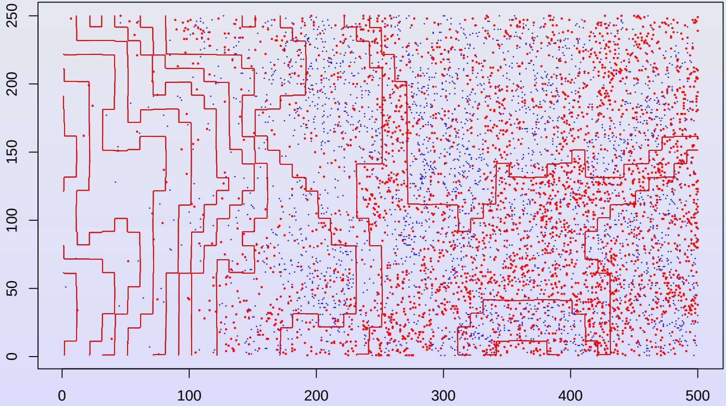
500x250 core of 1800x1800 grid

low species input $1.5x10^{-7}$ (a new species every ~100 years)

9 species at equilibrium with stable abundances over 10^6 years

Simulated niche-partitioning

Species 108, Species 64



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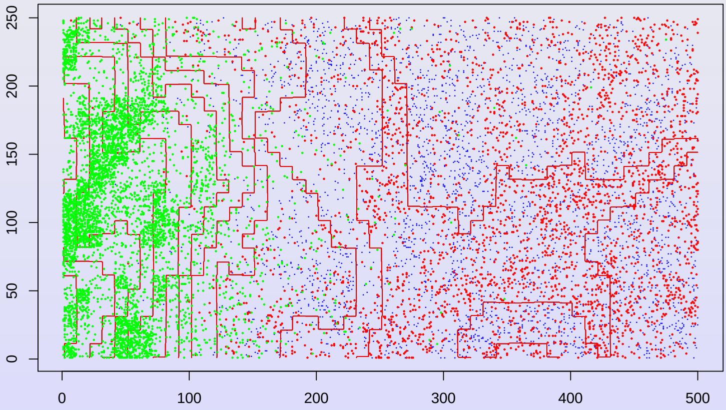
Simulated niche-partitioning

Species 108, Species 64, Species 32



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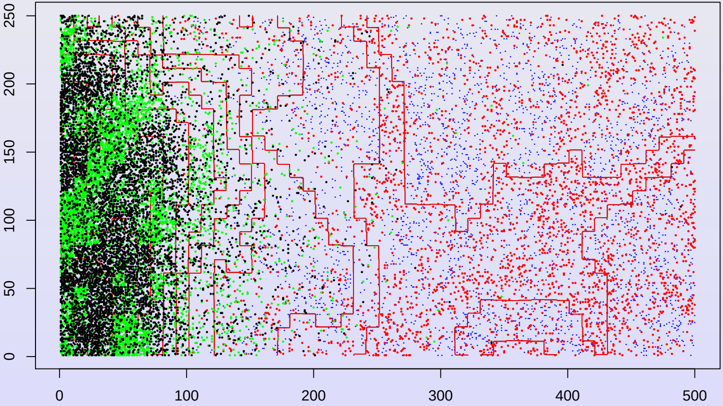
Species 108, Species 64, Species 32, Species 39



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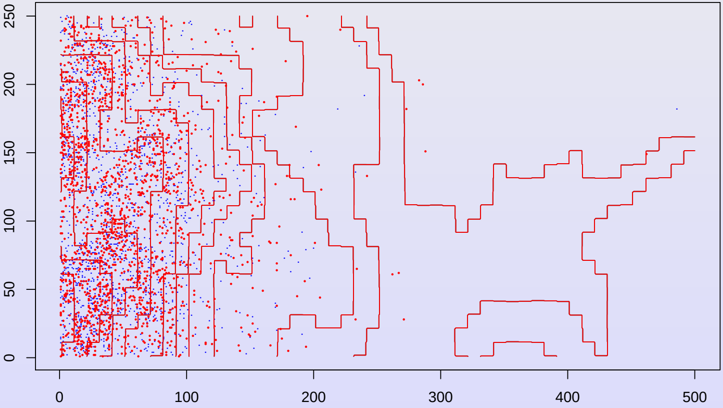
Species 19 and *8* share a niche and disperse well



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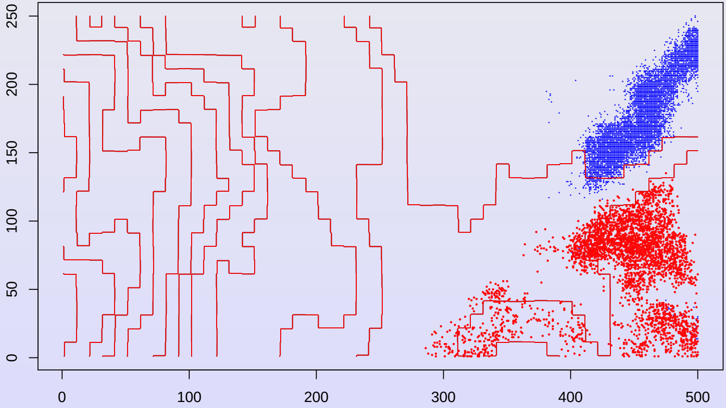
85 species with drifting abundances

Species 313 and *79* share a niche and disperse poorly



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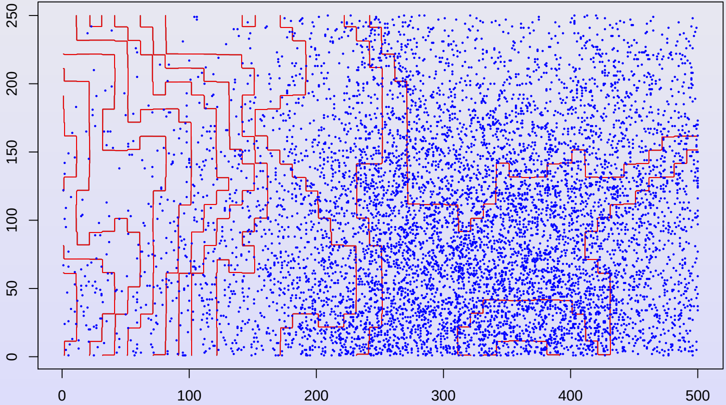
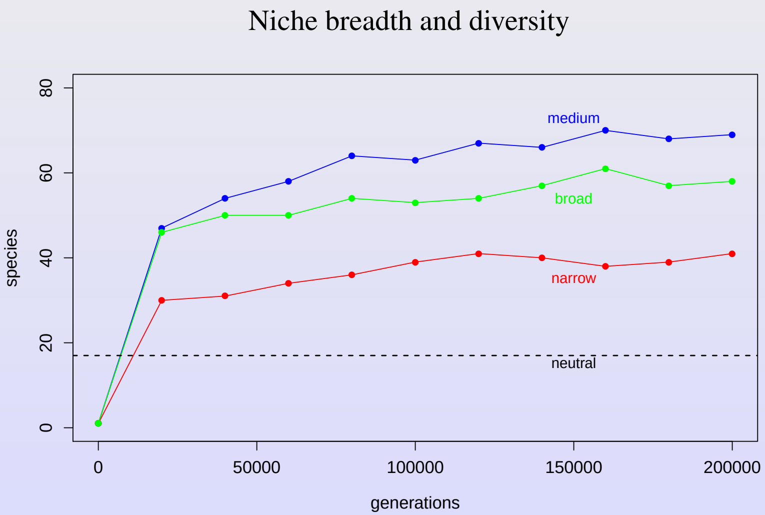


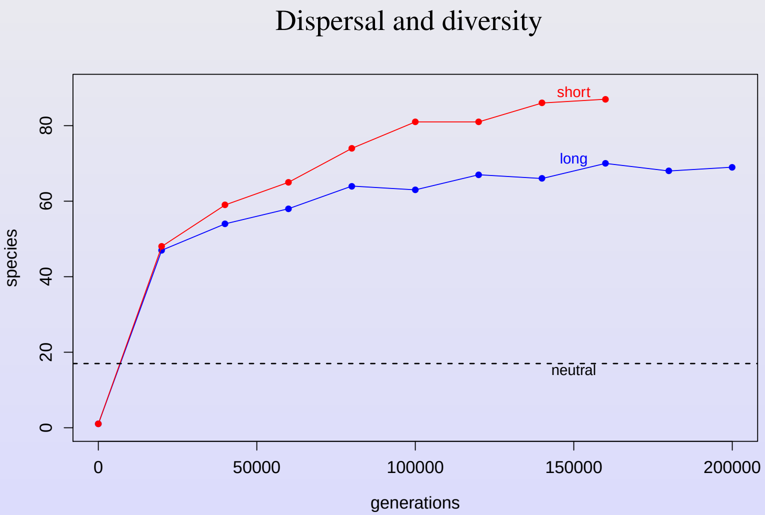
good diserpsal
high species input
weak niche differences
delayed maturation

Niche-driven species diversity



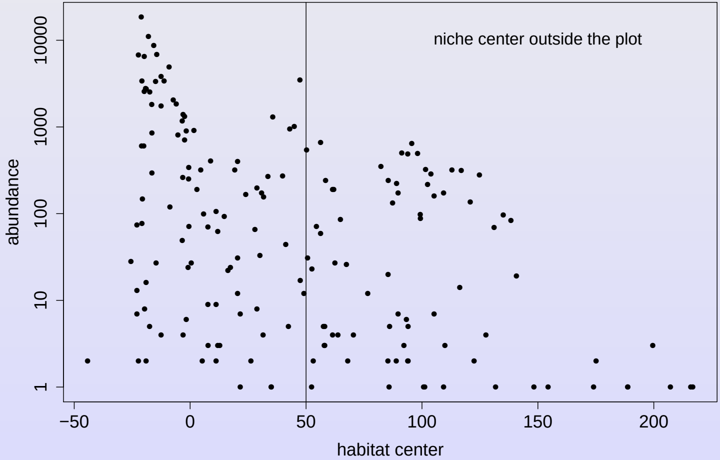
- low species input insufficient to maintain diversity
- identical niche strength

Niche-driven species diversity



- poor dispersal enhances diversity in niche-driven system
- it reduces diversity in input-driven system

Many simulated species have niche center outside the plot



- trait is elevation preference
- right section means preference is outside the plot

Diversity maintained by species input

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- Diversity can be very high
- Many rare species
- Species traits weakly related to abundance
- Species differences are unimportant to diversity

Diversity maintained by niche partitioning

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- At local scale, diversity is at best moderate
- Few rare species
- Species traits strongly related to abundance
- Coexistence theories matter and should predict diversity

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Diversity maintained by species input

Real forests

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- Many rare species
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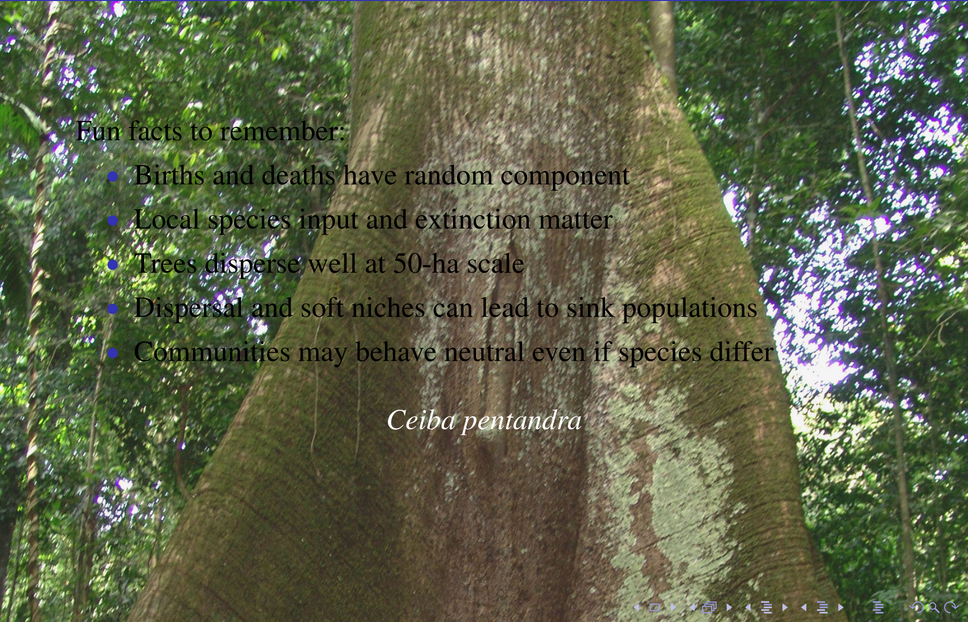
Diversity maintained by niche partitioning

Fun facts to remember:

- Births and deaths have random component
- Local species input and extinction matter
- Trees disperse well at 50-ha scale
- Dispersal and soft niches can lead to sink populations
- Communities may behave neutral even if species differ

Conclusions

Stochastic neutral and non-neutral communities



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Ceiba pentandra