

Motivation
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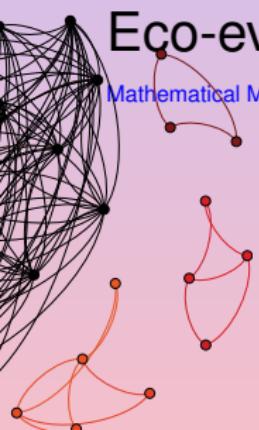
Results
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Swiss Federal Institute of Aquatic Science and Technology

Eco-evolutionary diversification dynamics

Mathematical Models in Ecology and Evolution, Paris, July 8-10, 2015



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- ▶ Joining neutral diversification models with more realistic speciation models

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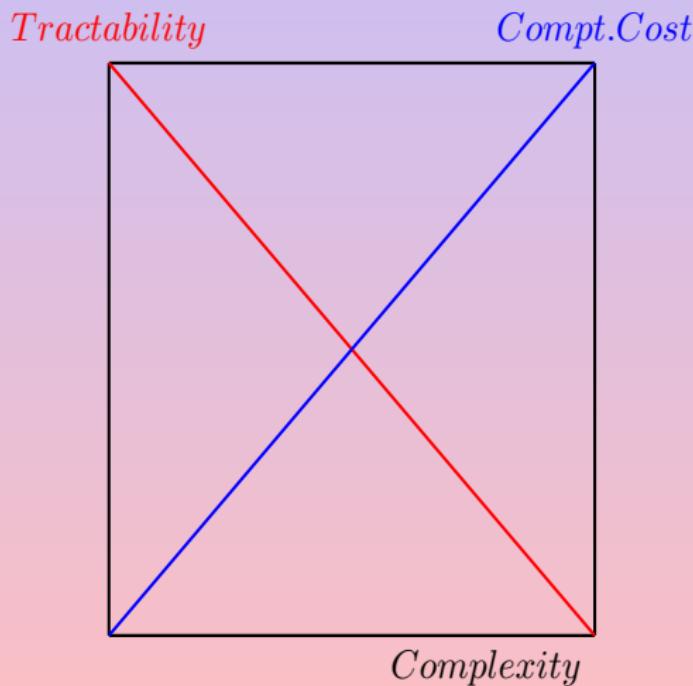
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- ▶ Joining neutral diversification models with more realistic speciation models
- ▶ Connecting microevolutionary processes to large scale patterns of biodiversity

Tractability and replicability



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Tractability and replicability

Models of speciation

Table	Glossary of mathematical notation used in Doebeli and Dieckmann (2003). Nature, 421:259-264. Last column clarifies whether the parameter is fixed, <i>f</i> , or evolves, <i>e</i> , during the simulations.	
Notation	Definition	Dynamics
u	Continuous quantitative trait in the asexual model between $0 \leq u \leq 1$	<i>e</i>
u	In the sexual model ecological ($0 \leq u \leq 1$), marker ($0 \leq u \leq 1$), and mating ($-1 \leq u \leq +1$) phenotypes are determined each by l diallelic diploid loci with additive effects and free recombination	<i>e</i>
n	Population size	<i>f</i>
(x, y)	Initial spatial location of each individual	<i>e</i>
σ_m	Mean movement of individual independent of location or phenotype	<i>f</i>
σ_K	It represents the width of the carrying capacity at its maximum	<i>f</i>
$K(u, x, y)$	Carrying capacity for ecological phenotype u at (x,y) is $K_o N_{\sigma_K}(u - u_o(x))$	<i>e</i>
u_o	Phenotype with maximal carrying capacity	<i>e</i>
$u_o(x)$	Phenotype u_o varies linearly with spatial dimension x ; y dimension is ecologically neutral	<i>e</i>
σ_c	Determines how fast the intensity of competition declines with phenotypic distance	<i>f</i>
σ_s	Determines how fast the intensity of competition declines with spatial distance	<i>f</i>
ν_r	Reversal mutation rate	<i>f</i>
$n_{eff}(u, x, y)$	Effective density experienced by an individual $i(u, x, y) = \frac{1}{2\pi\sigma_d^2} \sum N_{\sigma_u}(\Delta u)N_{\sigma_d}(\Delta d)$	<i>e</i>
b_i	Birth rate of individual i depends both on the number of other individuals in its neighbourhood and on their phenotypes. Asexual, $b_i = b$ and sexual, $b_i = b/(1 + c/n_p)$ where $n_p = \sum_{j=1}^n p_{ij} q_{ij}$ and c is the cost strength	<i>e</i>
d_i	Death rate of individual i depends both on the number of other individuals in its neighbourhood and on their phenotypes: $d_i = n_{eff}(u, x, y)/K(u, x, y)$.	<i>e</i>
B	Total birth rate	<i>e</i>
D	Total death rate	<i>e</i>
M	Total movement rate	<i>e</i>
b_i/B	Probability of individual i to have an offspring	<i>e</i>
d_i/D	Probability of individual i to die	<i>e</i>
m_i/M	Probability of individual i to move	<i>e</i>
a	The slope of the environmental gradient	<i>f</i>

Models of speciation

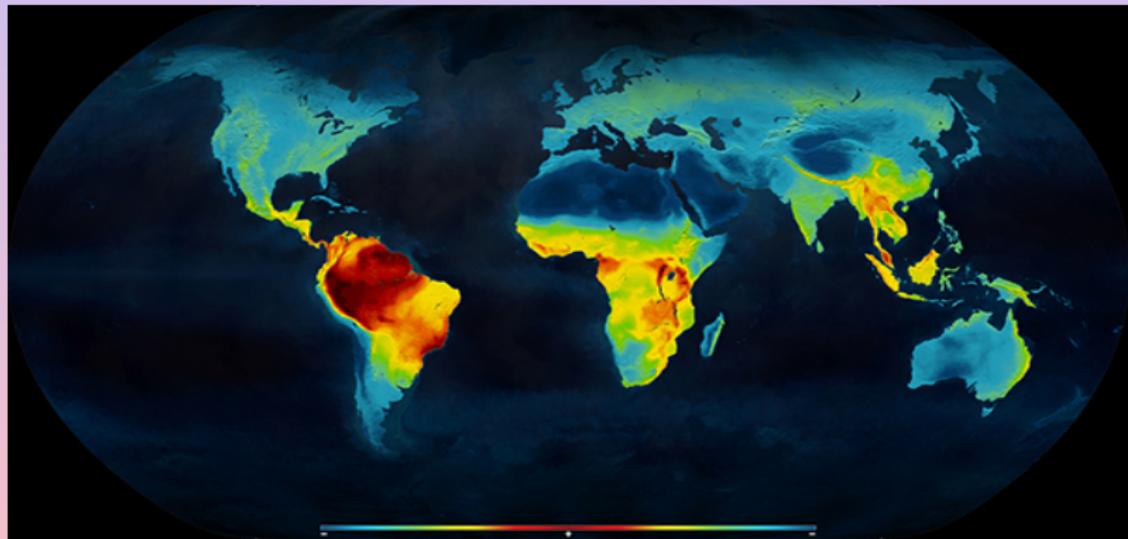
Table

	Glossary of mathematical notation used in Gavrilets and Vose (2005). PNAS, 102:18040-18045. Last column clarifies whether the parameter is fixed, <i>f</i> , or evolves, <i>e</i> , during the simulations: This is a nonoverlapping and discrete generations model. The life cycle consists of viability selection, preferential dispersal of surviving adults among neighboring patches and random mating within the patch.	
Notation	Definition	Dynamics
θ_i	Environmental factor $i = (1, 2, \dots, k)$. Each of these factors can take only two states, so each patch belongs to one of the 2^k possible ecological niches. Authors use $k = 3$ in a maximum system size of 32x32 patches	<i>e</i>
x_i	Ecological characters for each individual. Authors use $k = 3$.	<i>f</i>
y_i	Habitat Preference. Authors use $k = 3$.	<i>f</i>
M	The number of microsatellite loci in a multiallelic neutral loci genome. Authors use 8 loci	<i>f</i>
L	The number of loci per trait. Maximum explored was 16	<i>f</i>
K_{init}	The initial number of adults in the upper left corner of the system with all individuals identical homozygotes with all traits exactly at 0.5	<i>f</i>
μ	Mutation rate for the loci controlling ecological and preference traits and μ_n for the microsatellite loci	<i>f</i>
ϵ	Patch extinction rate	<i>f</i>
w_i	$w_i = x_i - \theta_i $, the fitness component of each individual controlled by the ecological character x_i in the i th environmental factor	<i>e</i>
w	$w = w_1 w_2 \dots w_k$, the overall fitness	<i>e</i>
p_i	$p_i = y_i - \theta_i $, the preference component of each individual controlled by the preference character y_i in the i th environmental factor	<i>e</i>
p	$p = p_1 p_2 \dots p_k$, the overall preference for an ecological niche	<i>e</i>
σ	The strength of selection	<i>f</i>
K	Carrying capacity controlled by the overall fitness	<i>e</i>
K_o	Maximum carrying capacity	<i>f</i>
b	The average number of offspring per female	<i>f</i>
N	The number of juveniles in the patch	<i>e</i>
a_j	Maximum possible habitat preference	<i>f</i>
N_e	The effective population size of the juveniles	<i>e</i>
y_{api}	The i th haplotype in the p th patch of the s th species	<i>e</i>
y	The vector of expected allelic states	<i>e</i>
α, β, γ	The effects of species, patch, and the individual, respectively, and are assumed random, additive and independent	<i>f</i>
$\sigma_\alpha^2, \sigma_\beta^2, \sigma_\gamma^2$	Variance components of α, β , and γ	<i>f</i>
F_{ST}, F_{SC}, F_{CT}	Estimates of intraclass correlations using the Hamming distance on the pairs of haplotypes	<i>e</i>
R_{ST}, R_{SC}, R_{CT}	Estimates of intraclass correlations using the stepwise mutation model on the pairs of haplotypes	<i>e</i>

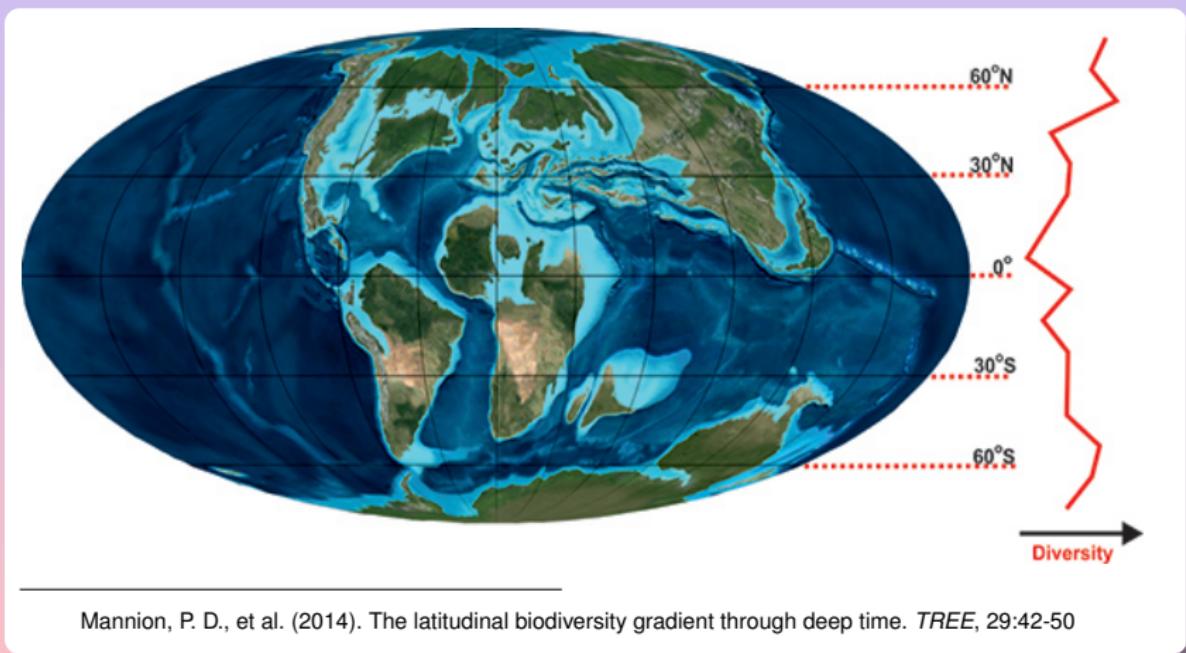
Models of speciation

Table	Glossary of mathematical notation used in van Doorn et al (2009). Science, 326:1704-1707. Last column clarifies whether the parameter is fixed, f , or evolves, e , during the simulations.	
Notation	Definition	Dynamics
h	Habitat type, A or B	f
N	Population size in habitat h	f
x	Ecological trait of an individual	e
μ_h	Optimal strategy in habitat h	f
q_h	Ecological performance which depends of the match between individual's ecological trait, x , and the optimal strategy in habitat h , μ_h	e
σ	The intensity of stabilizing selection within habitat h	f
p	Female's choosiness	e
t	male's strategy that determines the allocation of resources to expression of the ornament	e
$R(q_h)$	Total amount of resources for reproductive investment available to the male	e
s	Size of the male's ornament, and it is defined as $s = t q_h$	e
α	The strength of sexual selection	f
$exp(\alpha, p, s)$	Probability that a given female mates with a particular male	e
$m/2$	Per-capita migration rate per generation	f
β	The cost of ornament production	f
γ	The cost of female choosiness	f
N_e	effective population size in habitat h	e
L	Number of haploid loci and each locus can have two alleles	f
ν	mutation rate per allele per generation with phenotypic effect of magnitude $\delta x = 0.1$, $\delta p = 0.05$, and $\delta t = 0.1$	f
$w(x)_i$	Fitness of a rare mutant i with phenotype x	e
M	Transition matrix to track frequency changes of rare mutants in habitat A and B	e
f_i	Distribution of phenotypes among the offspring produced in habitat A at the end of a generation, where genotype classes are indexed by the number of + alleles i	e
a_i	Attractiveness of males with phenotype i , and it is defined as $a_i = \exp(\alpha p t w_i)$	e
k_p	Evolutionary rate of change of female preference	f
k_t	Evolutionary rate of change of male ornament investment	f

Latitudinal biodiversity gradient: Contemporary time



Latitudinal biodiversity gradient: Late Cretaceous

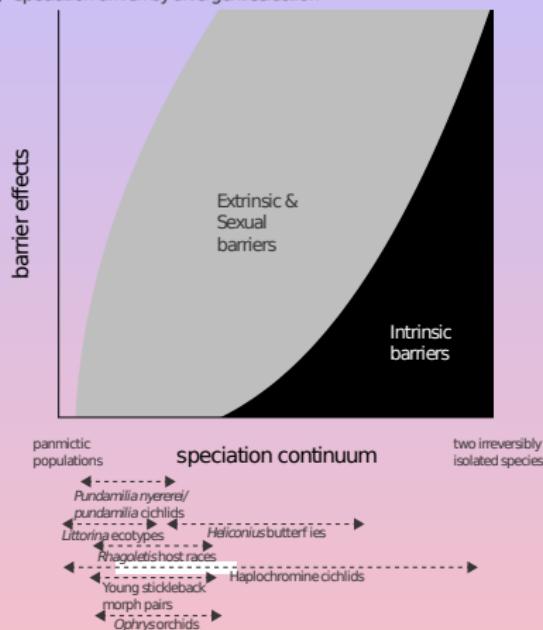


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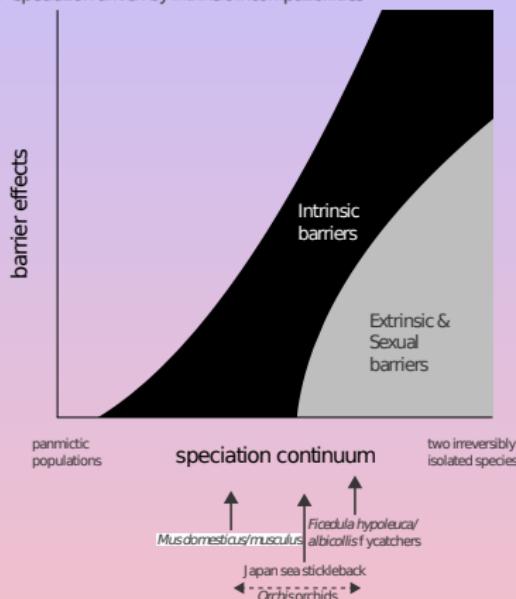
- ▶ Do neutral diversification models predict the biogeography of hot and cold spots?

Ecological and non-ecological speciation

a) Speciation driven by divergent selection



b) Speciation driven by intrinsic incompatibilities



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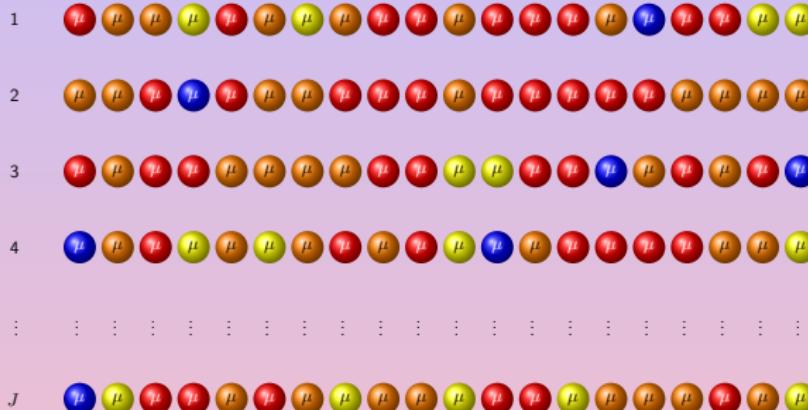
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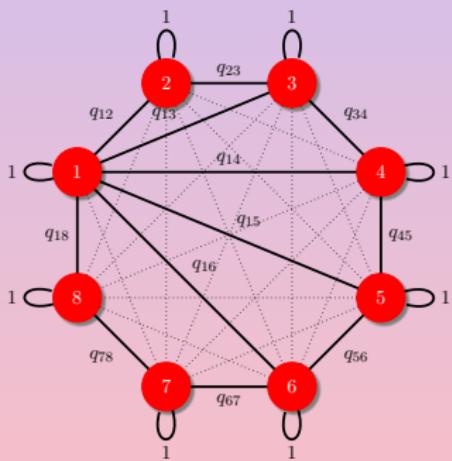
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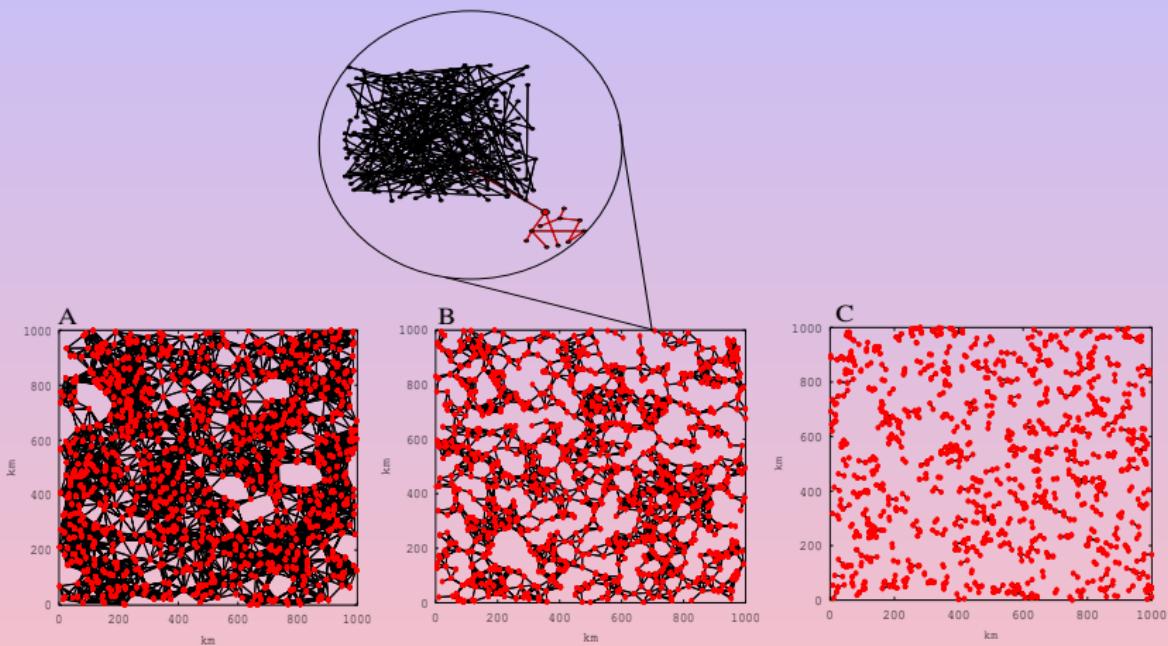
Population size, \mathcal{J} , Genome size, \mathcal{L} , and mutation rate, μ



Genomes in a mating graph (threshold, \mathcal{Q}_{min}); $Q = [q_{ij}]$ and $q_{ij} > \mathcal{Q}_{min}$ 

$$Q = \begin{bmatrix} 1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 \\ 1 & 1 & q_{12} & q_{13} & q_{14} & q_{15} & q_{16} & 0 & q_{18} \\ 2 & q_{21} & 1 & q_{23} & 0 & 0 & 0 & 0 & 0 \\ 3 & q_{31} & q_{32} & 1 & q_{34} & 0 & 0 & 0 & 0 \\ 4 & q_{41} & 0 & q_{43} & 1 & q_{45} & 0 & 0 & 0 \\ 5 & q_{51} & 0 & 0 & q_{54} & 1 & q_{56} & 0 & 0 \\ 6 & q_{61} & 0 & 0 & 0 & q_{65} & 1 & q_{67} & 0 \\ 7 & 0 & 0 & 0 & 0 & 0 & q_{76} & 1 & q_{78} \\ 8 & q_{81} & 0 & 0 & 0 & 0 & 0 & q_{87} & 1 \end{bmatrix}$$

Genomes in the landscape (threshold, D_{max}); $D = [d_{ij}]$ and $d_{ij} \leq D_{max}$



Gene flow, (\mathcal{M})

Symmetric gene flow

$$m_{ij}^k = \frac{\mathcal{M}}{d_{ij}} \quad (1)$$

Centripetal gene flow

$$m_{ij}^k = \begin{cases} \frac{\mathcal{M}}{d_{ij}} & \text{if } \sum_{l=1}^S d_{il} \leq \sum_{l=1}^S d_{jl}, \\ 0 & \text{if } \sum_{l=1}^S d_{il} > \sum_{l=1}^S d_{jl} \end{cases} \quad (2)$$

Centrifugal gene flow

$$m_{ij}^k = \begin{cases} \frac{\mathcal{M}}{d_{ij}} & \text{if } \sum_{l=1}^S d_{il} \geq \sum_{l=1}^S d_{jl}, \\ 0 & \text{if } \sum_{l=1}^S d_{il} < \sum_{l=1}^S d_{jl} \end{cases} \quad (3)$$

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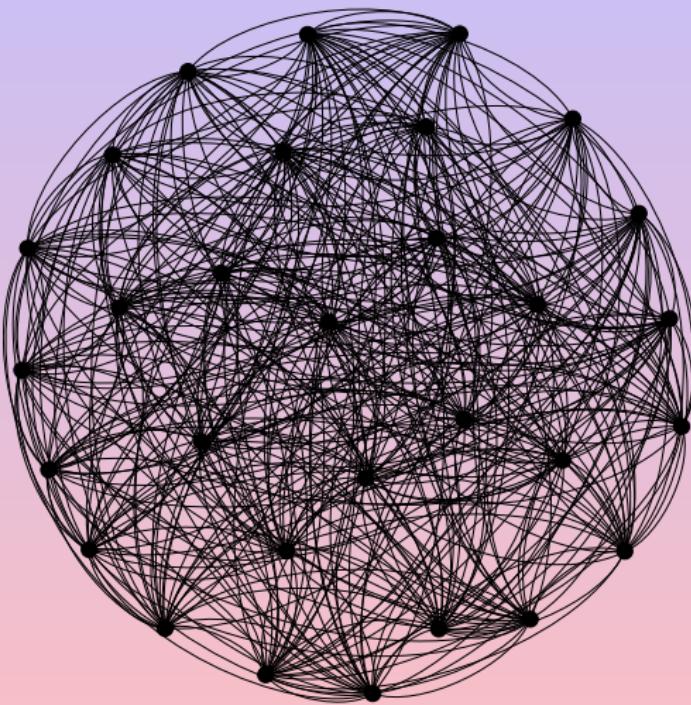
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Given \mathcal{J} , μ , \mathcal{Q}_{min} and $\mathcal{D}_{max} = 1$, do we find isolated clusters in the graph?



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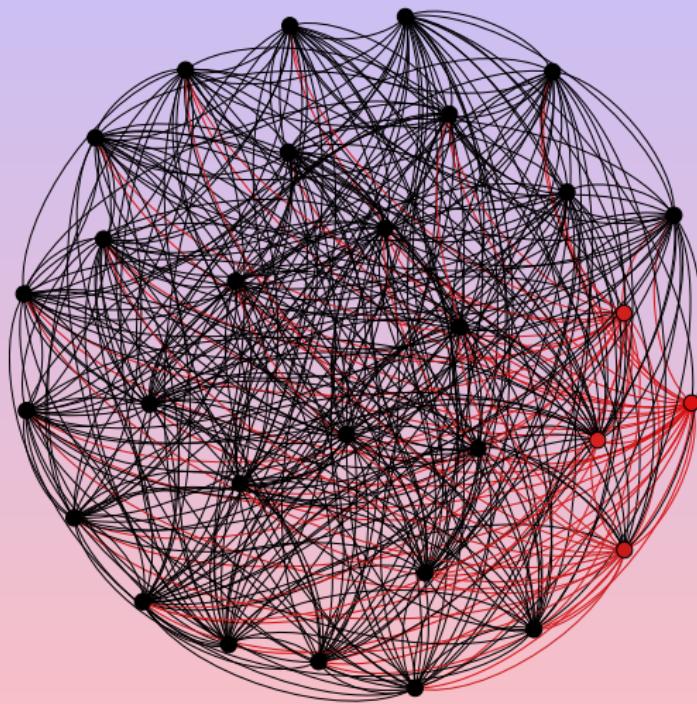
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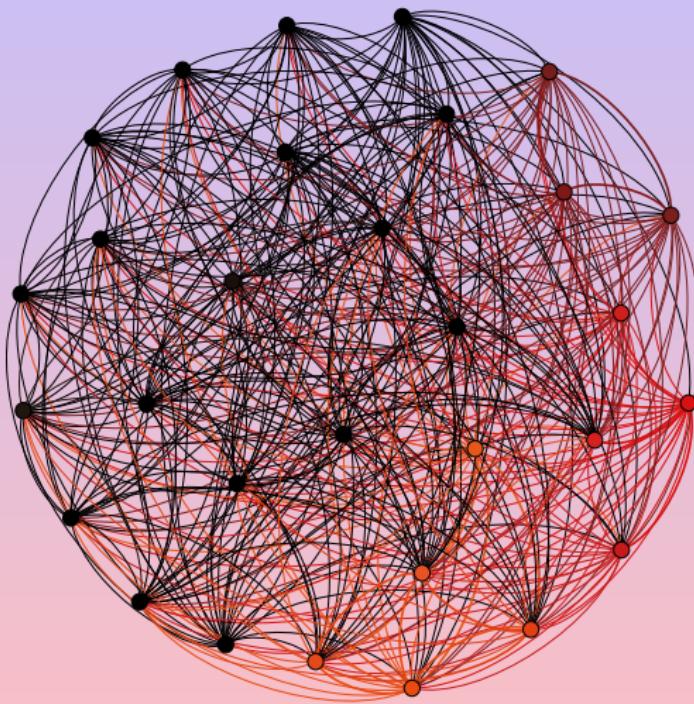
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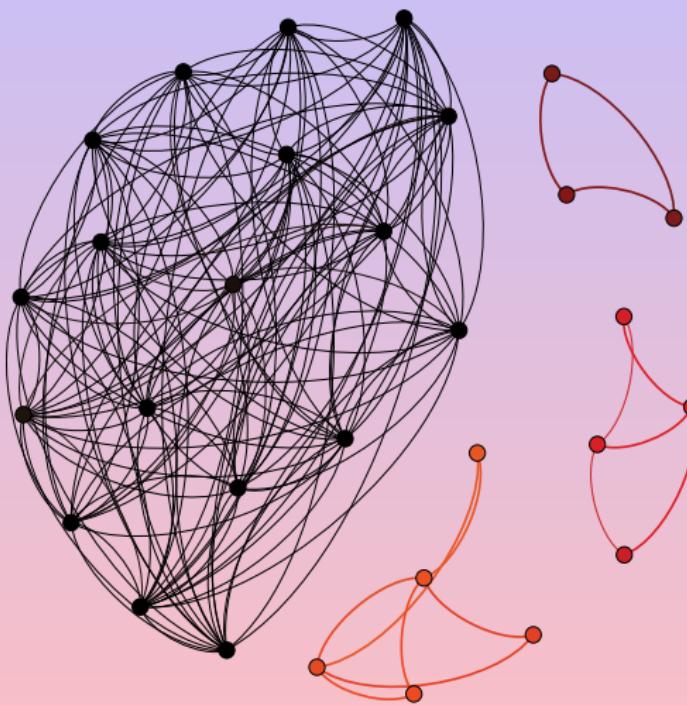
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Given \mathcal{J} , μ , \mathcal{Q}_{min} and $\mathcal{D}_{max} = 1$, do we find isolated clusters in the graph?



► Given \mathcal{J} , μ , and $\mathcal{Q}_{min} > Q^* \rightarrow Q^* = \frac{1}{4J\mu+1}$

Asexual reproduction: $\rightarrow n_{asex}^* = -\frac{\log(\mathcal{Q}_{min})}{2\mu}$

Sexual reproduction: $\rightarrow n_{sex}^* = \frac{\log(\mathcal{Q}_{min})}{-2\mu + \log[(\mathcal{Q}_{min}+3)/4]}$

Melián, C. J., et al. (2010). Frequency-dependent selection predicts patterns of radiations and biodiversity.
PLoS Comput Biol, 6(8):1000892.

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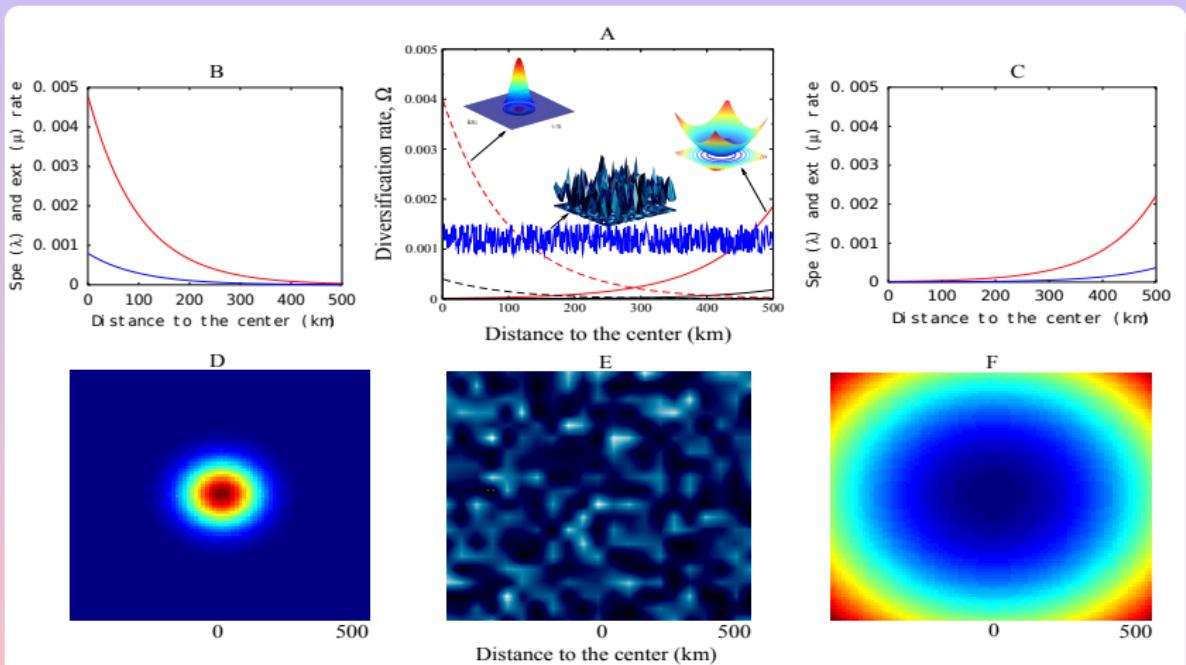
And $n_{asex}^ > n_{sex}^*$ in all cases,*

so $1/n_{sex}^ (\nu_{sex}) > 1/n_{asex}^* (\nu_{asex})$*

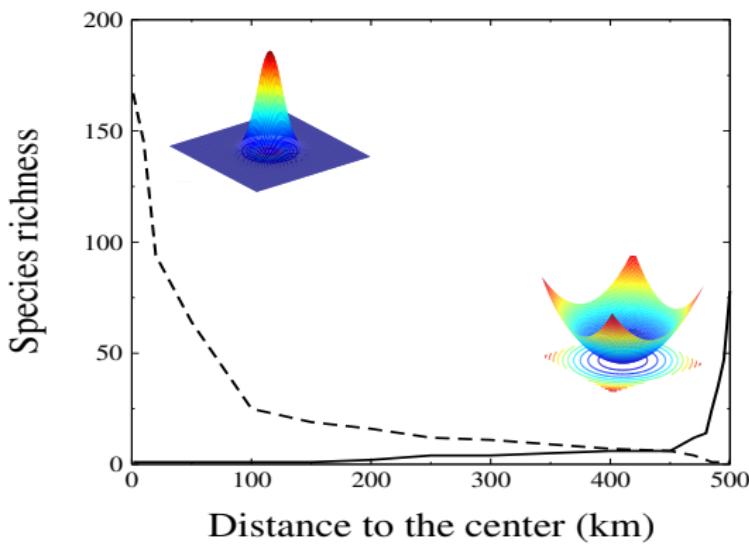
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Hot and cold spots ($\mathcal{J}, \mathcal{L}, \mu, Q_{min}, D_{max}, M$)



Hot spots and species richness



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- ▶ Merging neutral theory of molecular evolution to neutral biodiversity theory is at an incipient stage

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- ▶ Centripetal gene flow model predicts hot spots in the center of the distribution ranges of diversifying lineages

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- ▶ Merging neutral theory of molecular evolution to neutral biodiversity theory is at an incipient stage
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- ▶ Centripetal gene flow model predicts hot spots in the center of the distribution ranges of diversifying lineages
- ▶ **CHALLENGE:** Link models of hot and cold spot formation to the empirical patterns of latitudinal biodiversity gradient

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Thank you!

- ▶ Computing-scientist staff at NCEAS, University of California Santa Barbara.
- ▶ Swiss National Foundation