



# Modeling co-evolutionary dynamics of *L. pulmonaria* lichen symbiosis



Carrignon S, Ollé-Vila A, Adams J,  
Duran-Nebreda S

# Outline

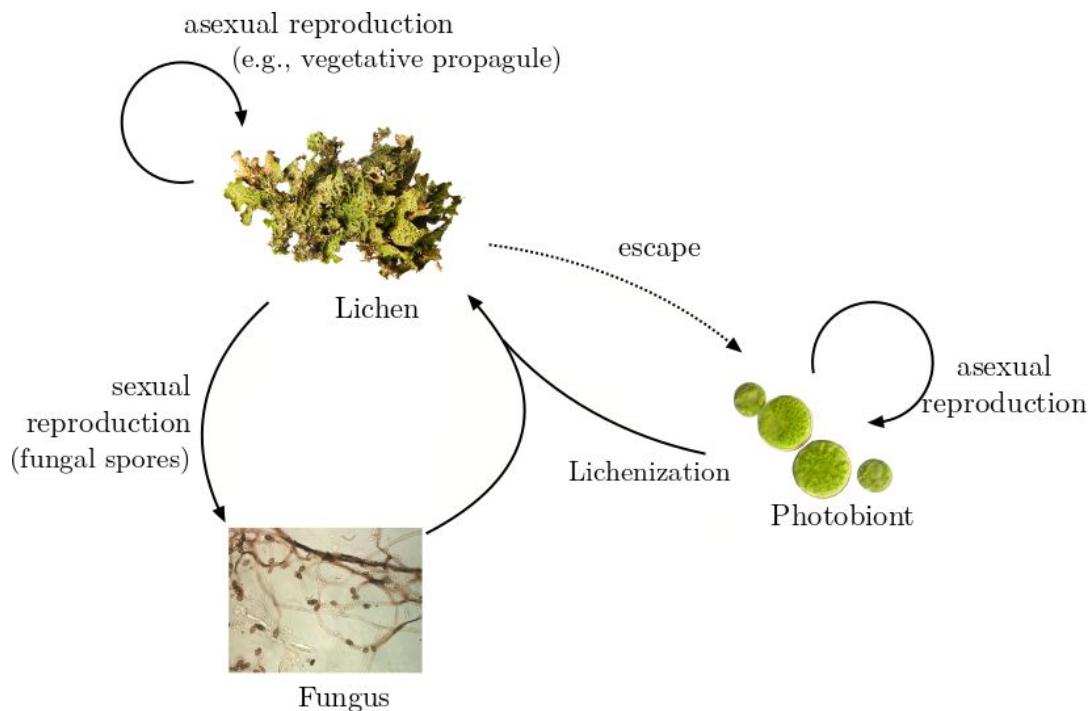
1. What is a lichen?
2. Computer Simulation, the “ECHO” model
3. Validation & Exploration

# What is a lichen?

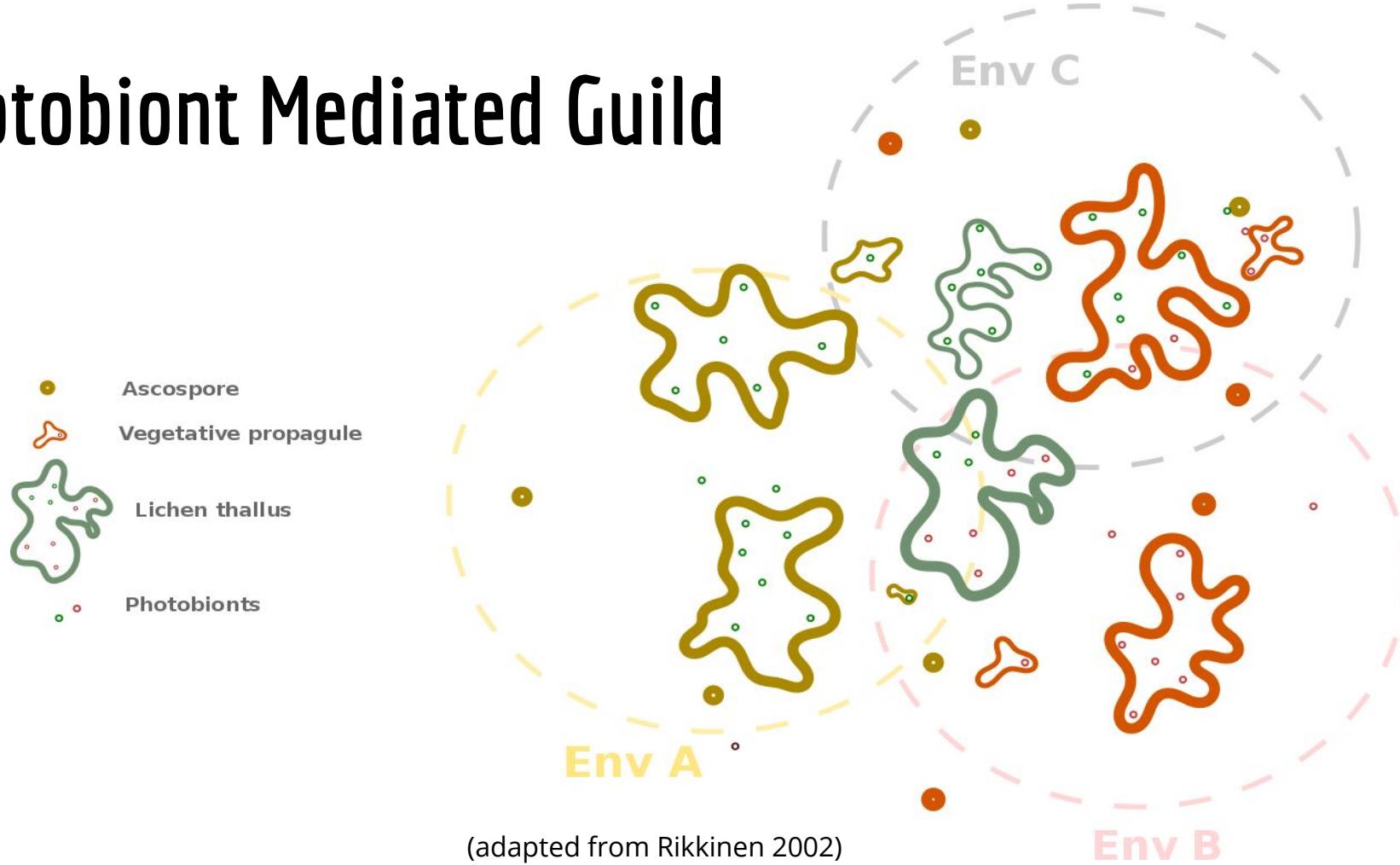
- Symbiosis between a fungus and a photobiont (cyanobacteria, algae).
- They thrive in different *niche*: trees/rocks, dry/humid, etc.
- Hyperdiverse (morphologically and genetically), performing numerous ecological functions.



# Lichen life cycle



# Photobiont Mediated Guild

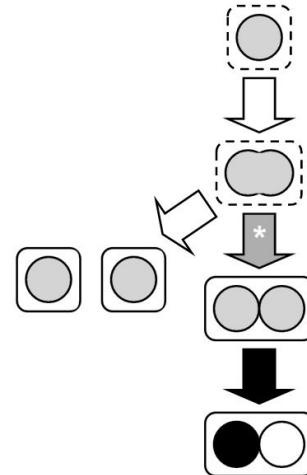


# Major Transition

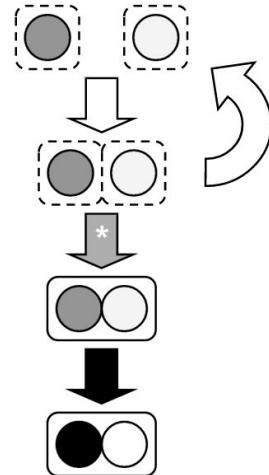
- Highly successful symbiotic interaction between widely different and coevolving partners.
- Levels of selection. A frozen stage of a major transition in evolution?

**What has shaped their coevolution and might continue to do so in the future?**

Reproductive Fission



Ecological Fusion



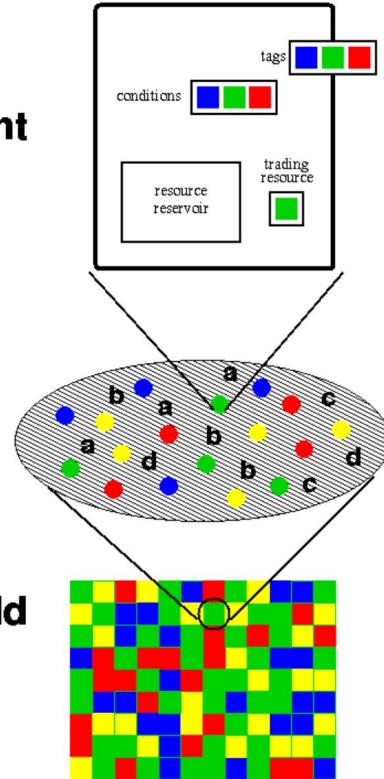
Kerr and Nahum (2011) *The Major Transitions in Evolution Revisited*.

# Empirical Challenge

- Studies at large spatial and temporal scales
- Complex evolutionary dynamics involving heterogeneous and delicate biological entities

# The ECHO model

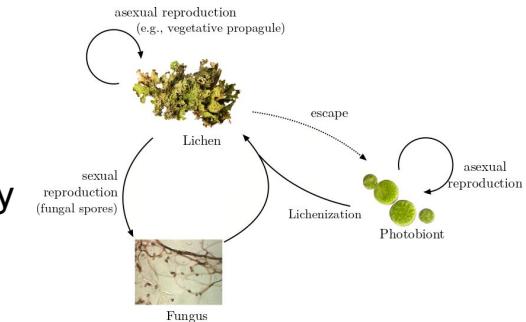
Agent



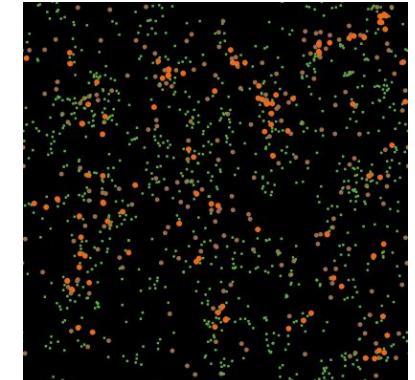
fungi tag: 010101000101001

algae tag: 110101011001101

the more similar the more likely  
that lichen will be formed.



- ABM consisting of entities and a simplified spatial domain.
- Agents contain a genotype (symbol string) that mutates and directs interactions between entities (combat, trade, mating, etc.).

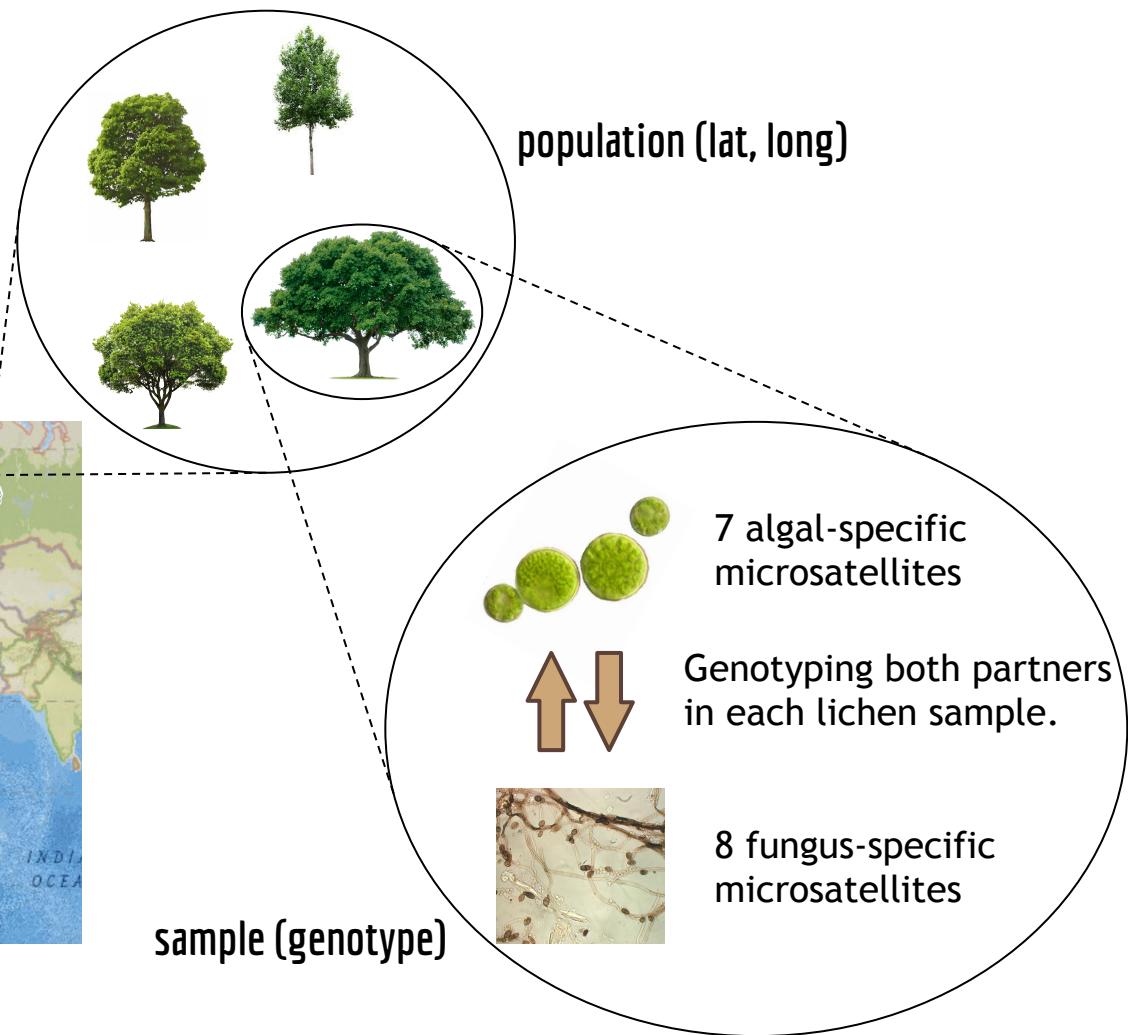


# Validation step

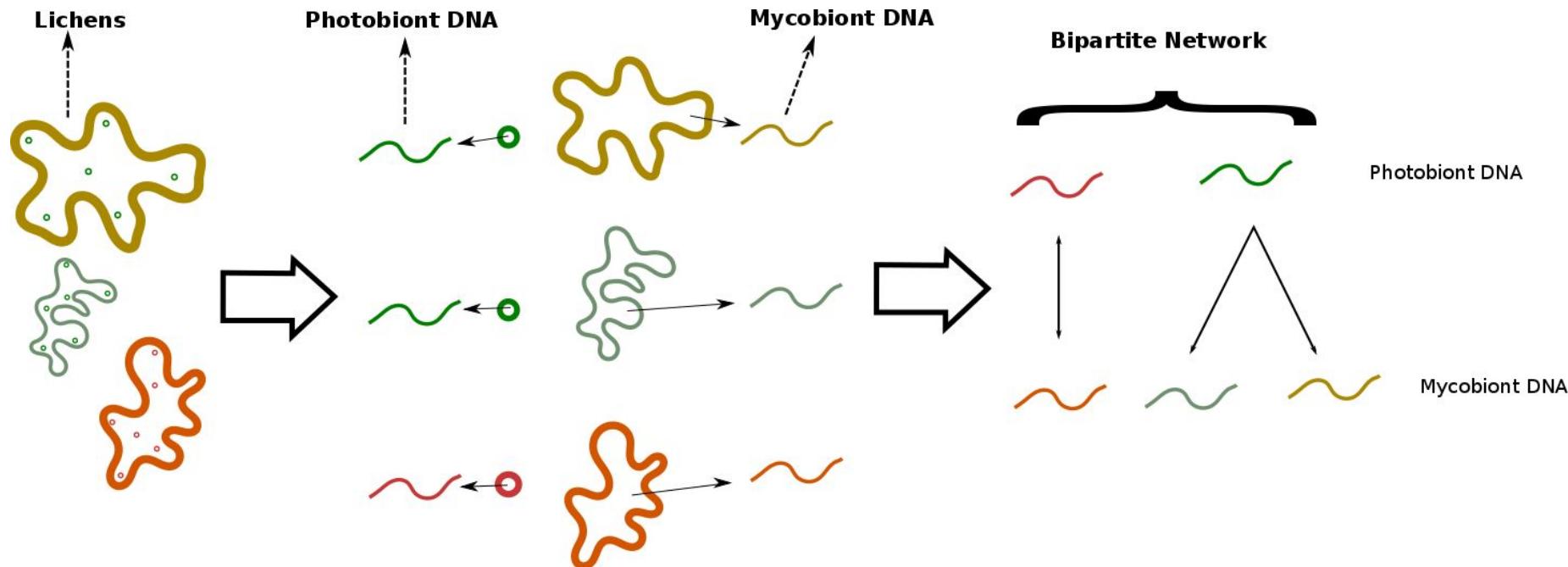
Verify that the model is able to reproduce properties observed in real systems  
(data set used: Dal Grande et al. 2012)

# Data set

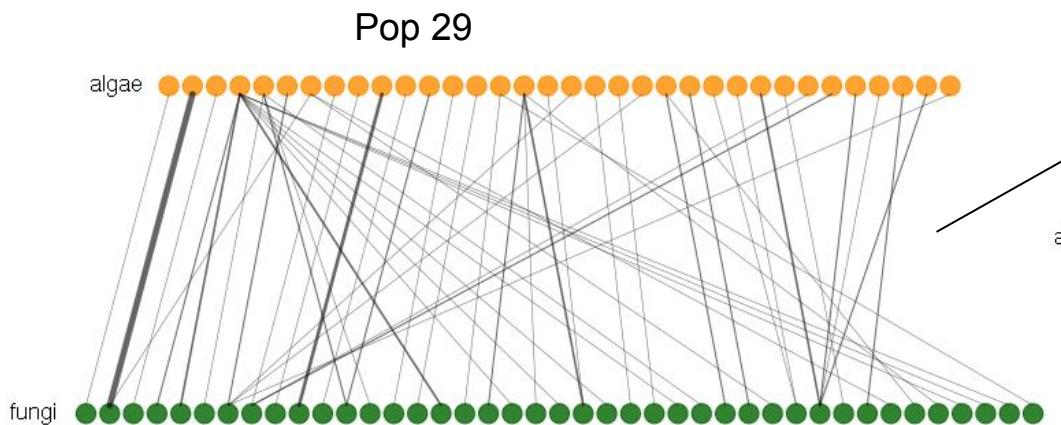
*L. Pulmonaria*  
(Dal Grande *et al.* 2012)



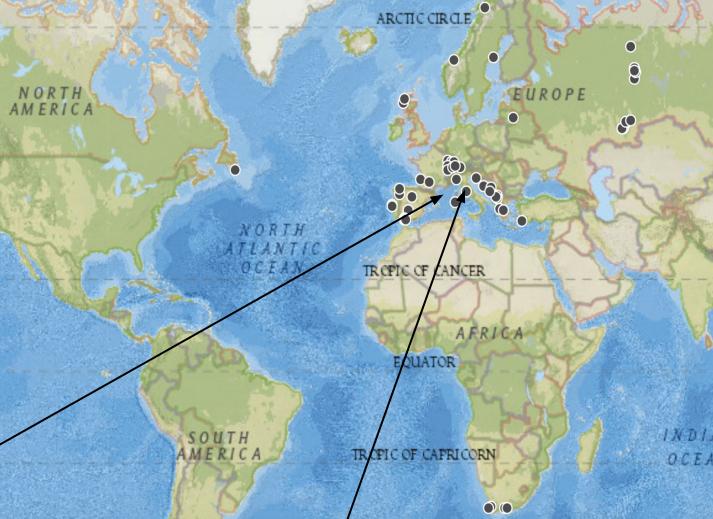
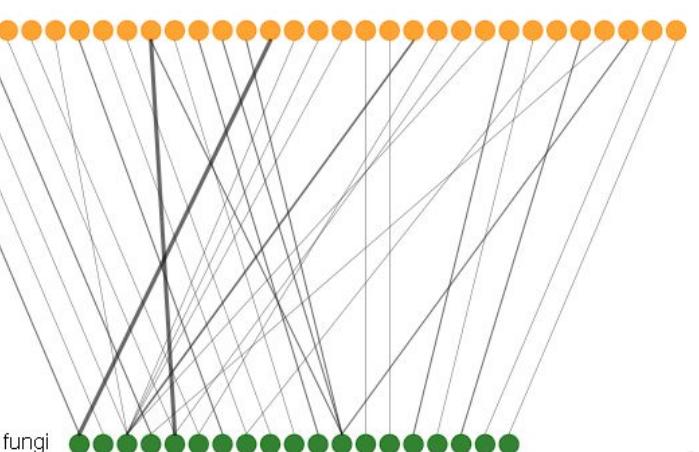
# Symbionts bipartite network



# Symbionts bipartite network

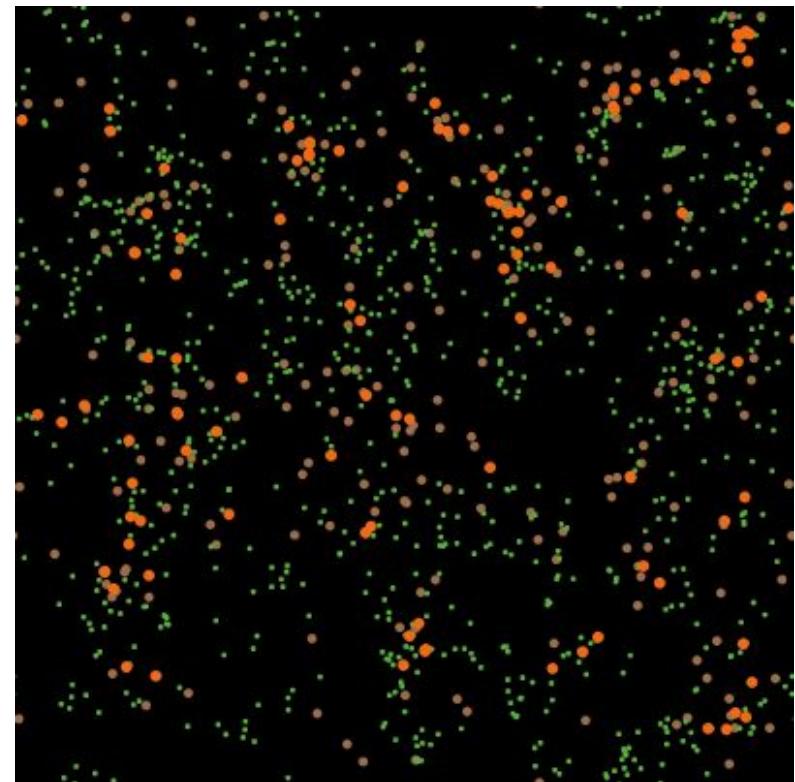


Pop 31



# Scale Model Result

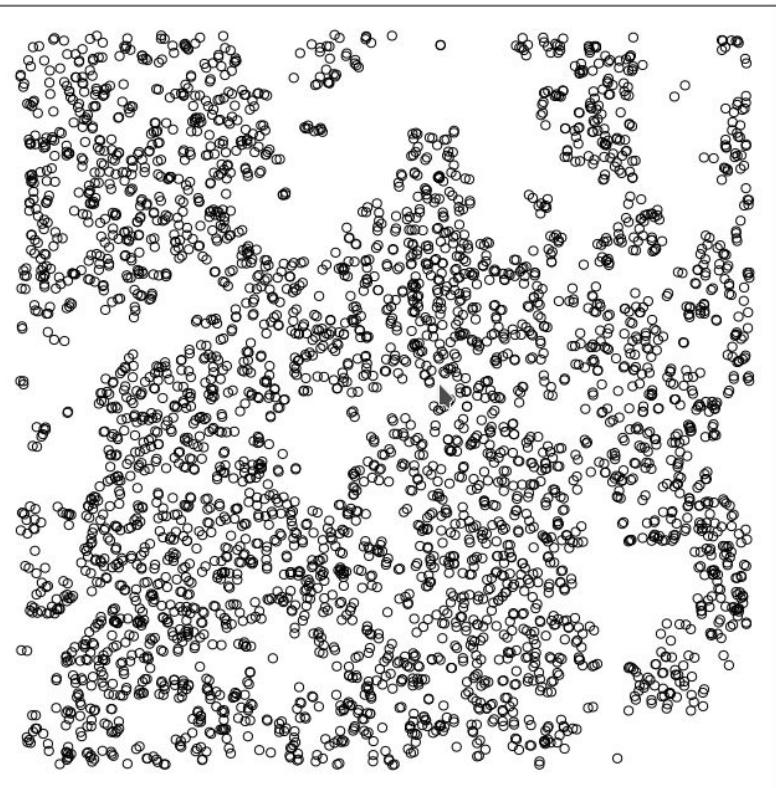
Original model result:



# Scale Model Result

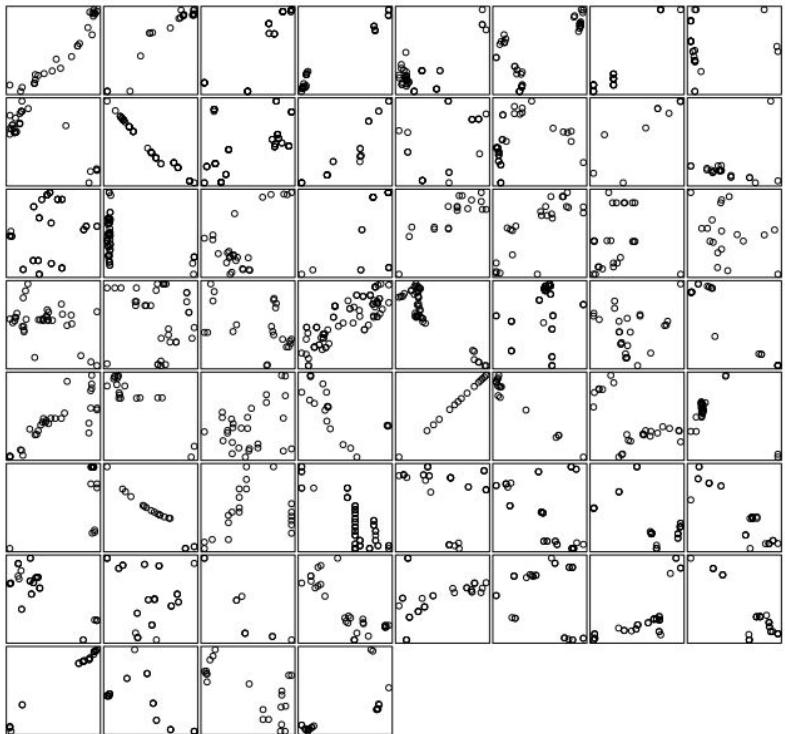
Original model result:

Model output  
after 10000 timestep

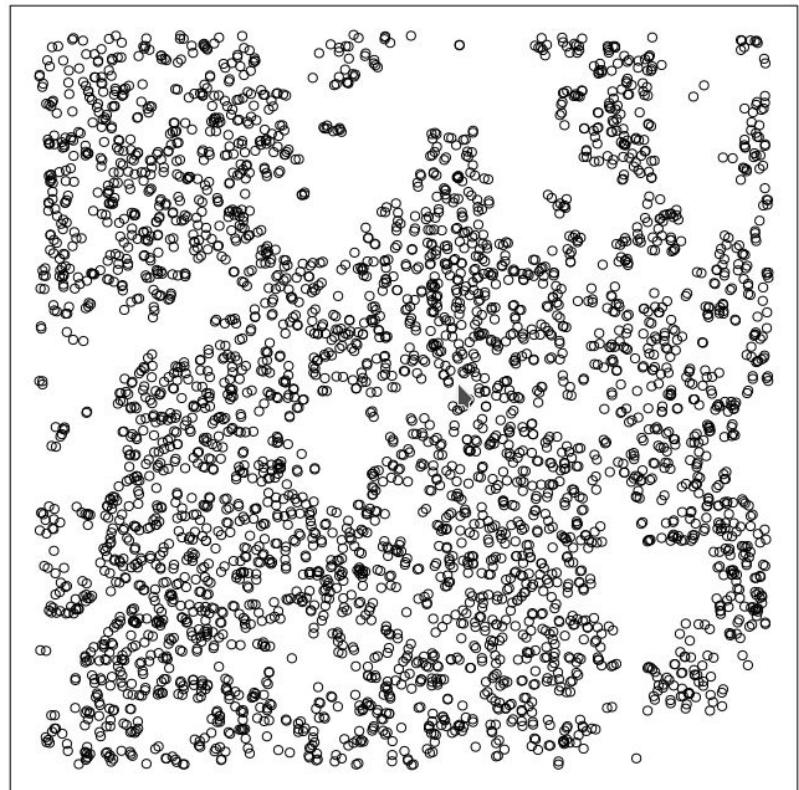


# Scale Model Result

Spatial Dispertion of Sample  
within each pop (real Data)

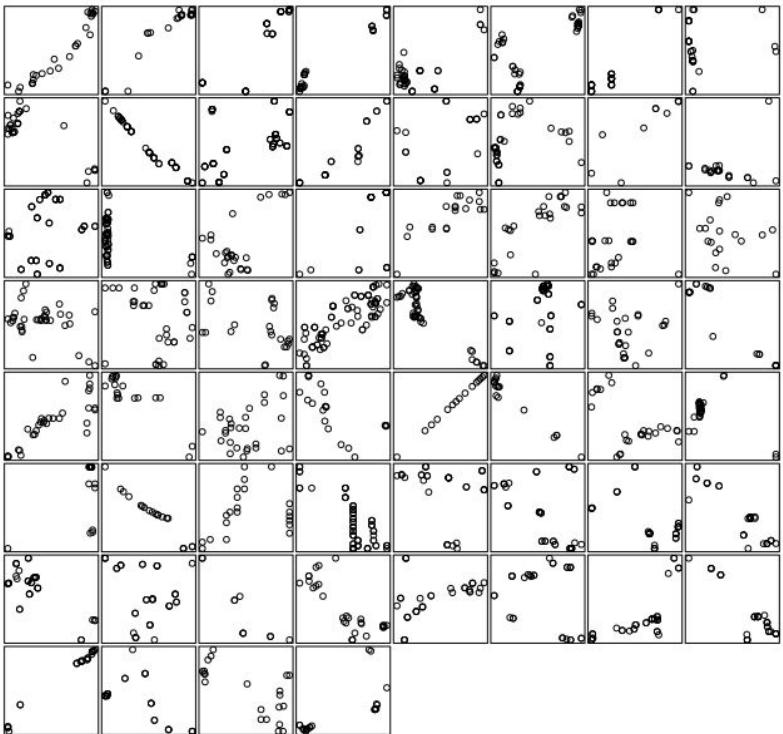


Model ouptut  
after 10000 timestep

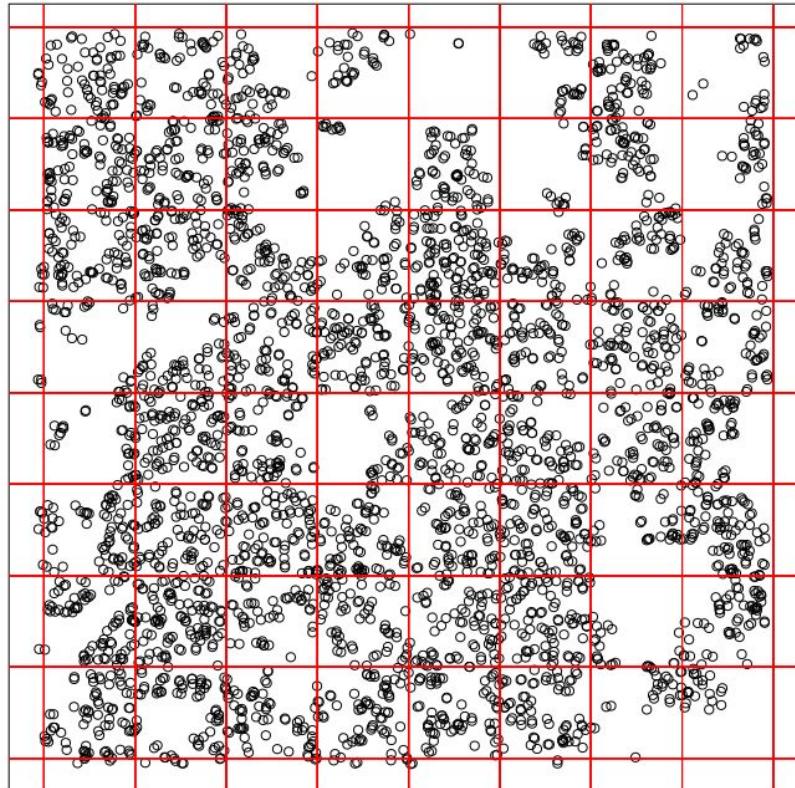


# Scale Model Result

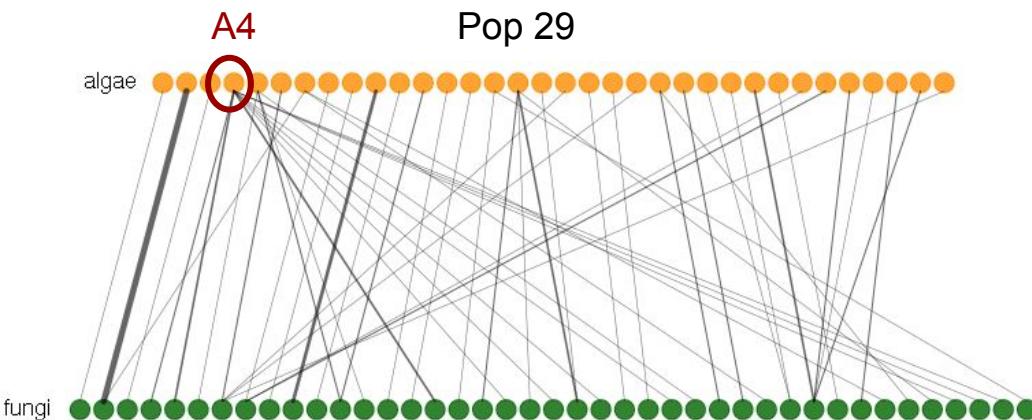
Spatial Dispertion of Sample  
within each pop (real Data)



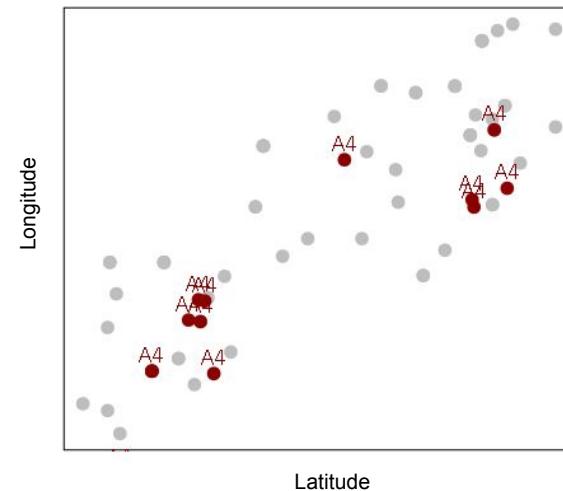
Model ouptut  
after 10000 timestep



# Population Structure



Spatial repartition of lichens  
within Pop 29



# Population Structure

## Betweenness centrality

Importance of a node as a connector between different parts of the network. Nodes with BC>0 connect areas of the network that would otherwise be sparsely or not connected at all. Species which are important to the cohesiveness of the network will have a positive BC.

$$BC_i = \sum_{jk} \frac{g_{jk}(i)}{g_{jk}}$$

$g_{jk}(i)$ , number of shortest paths between  $j$  and  $k$  going through  $i$

$g_{jk}$ , number of shortest paths linking  $j$  and  $k$

## Goal: Link node properties with spatial structure

Newman M. E. J. Networks: an introduction. Oxford University Press, 2010

Opsahl T, Agneessens F, Skvoretz J. Node centrality in weighted networks: Generalizing degree and shortest paths. Social Networks 32 (2010) 245-251

# Population Structure

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$$BC_i^{w\alpha} = \sum_{jk} \frac{g_{jk}^{w\alpha}(i)}{g_{jk}^{w\alpha}}$$

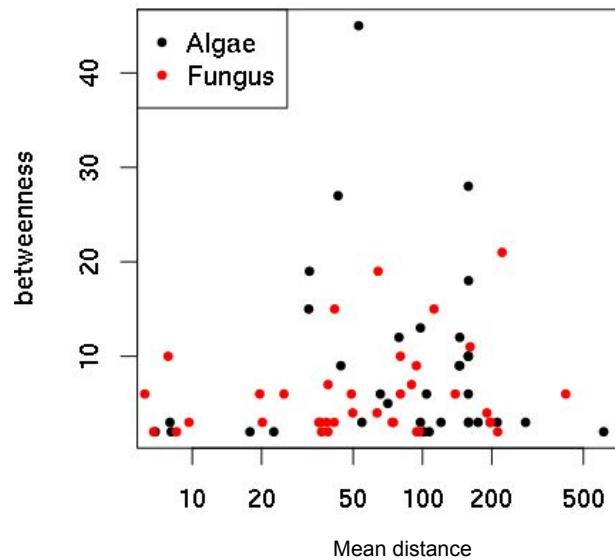
$$d^{w\alpha}(i, j) = \min\left(\frac{1}{(w_{ih})^\alpha}\right) + \dots + \frac{1}{(w_{hj})^\alpha}$$

## Goal: Link node properties with spatial structure

# Population Structure

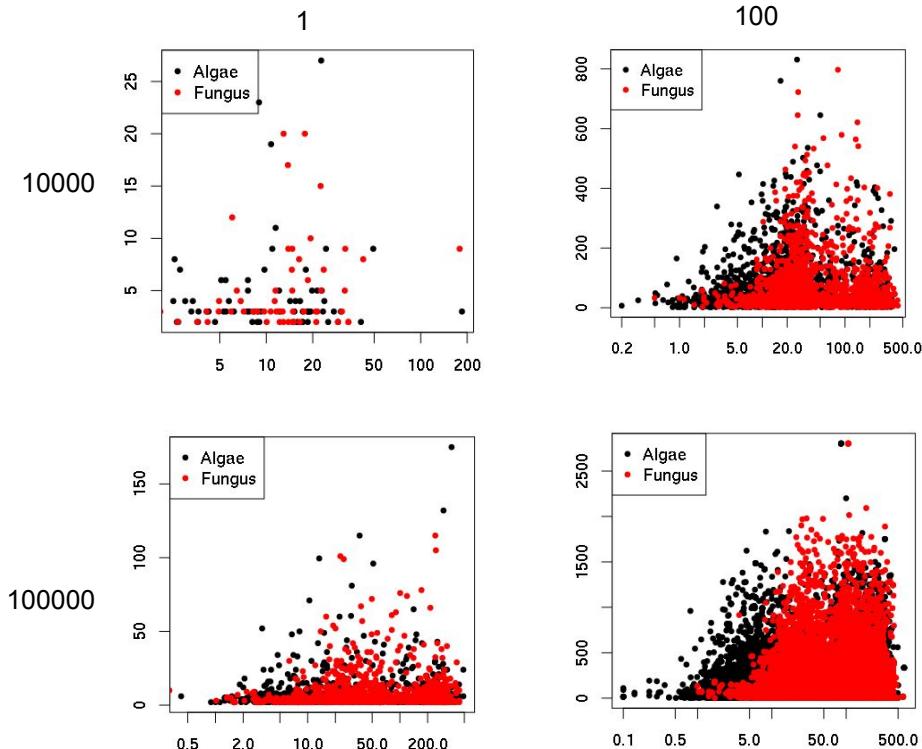
Betweenness Centrality vs Mean distance

Dal Grande 2012



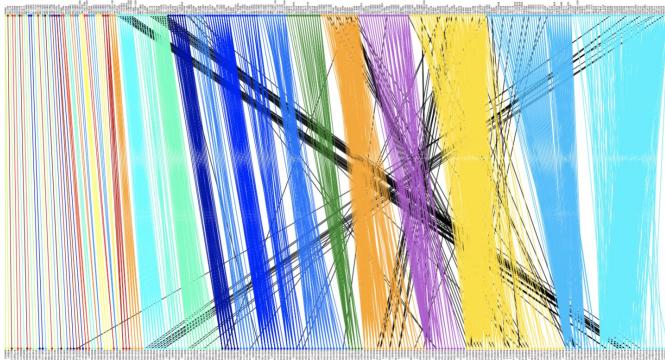
Timestep

Sexual reproduction



# Population Structure

## Modularity



$$Q = \frac{1}{|E|} \sum_{ij} (B_{ij} - \frac{k_i d_j}{|E|}) \delta(g_i, h_j)$$

$|E|$ , number of links in the network

$B_{ij}$ , adjacency matrix

$k_i, d_j$ , degree of nodes  $i$  and  $j$

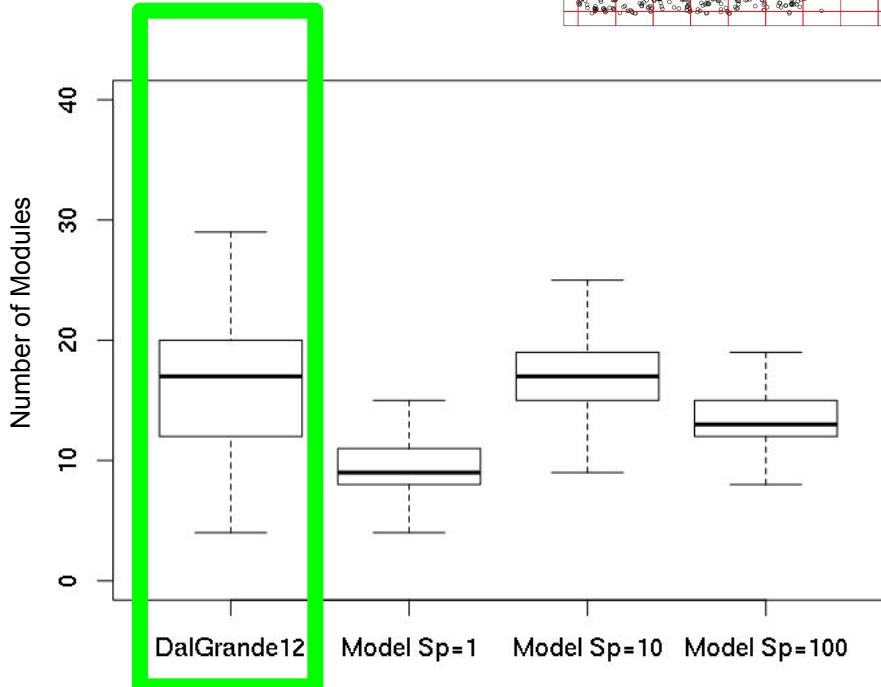
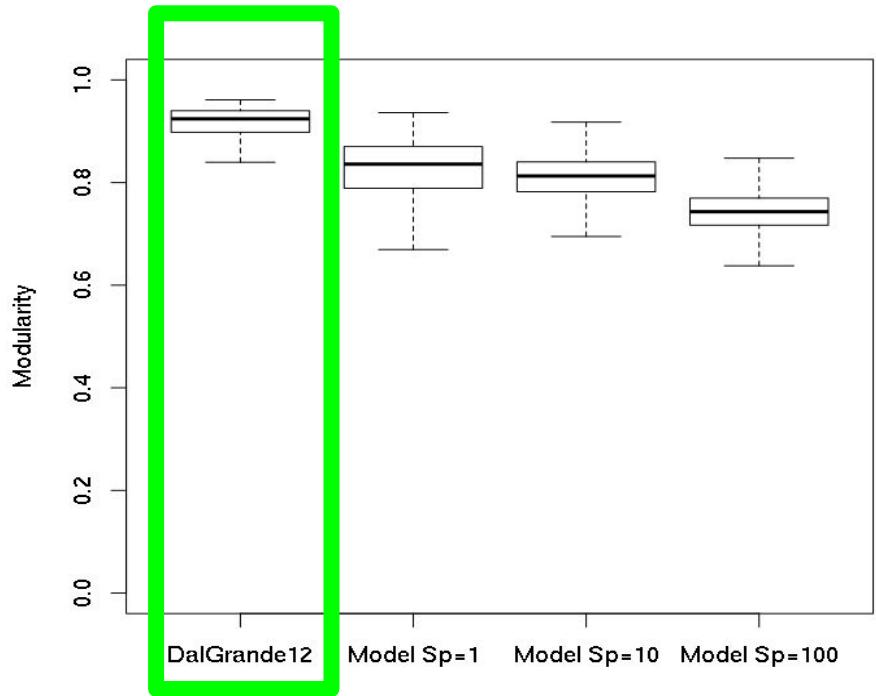
$g_i, h_j$ , modules indices of nodes  $i$  (belongs to set R) and  $j$  (belongs to set C)

Newman, M. E. J. 2006. Finding community structure in networks using the eigenvectors of matrices. Physical Review E, 74, 036104.

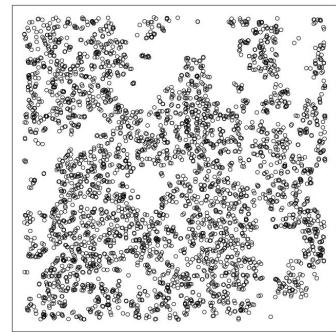
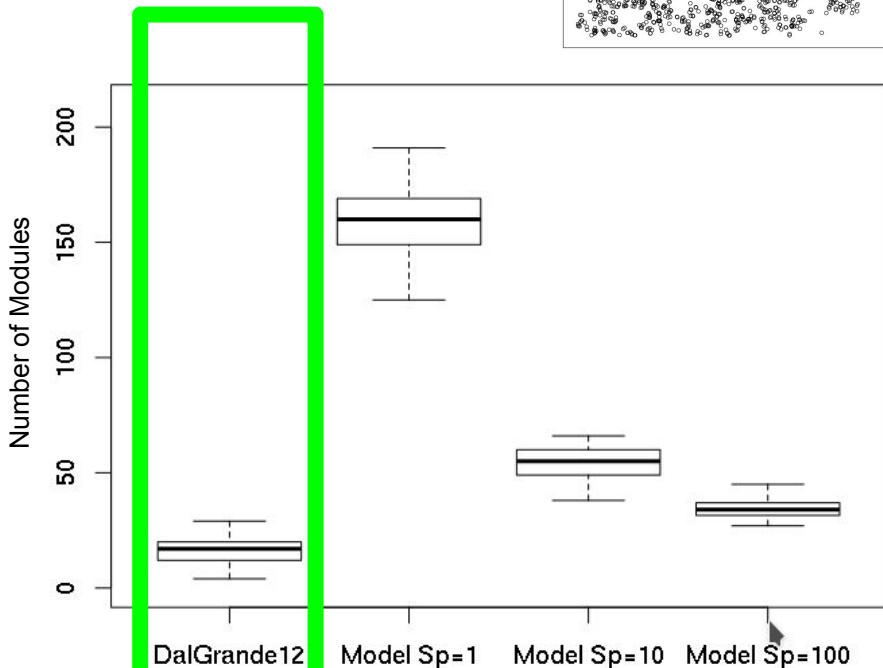
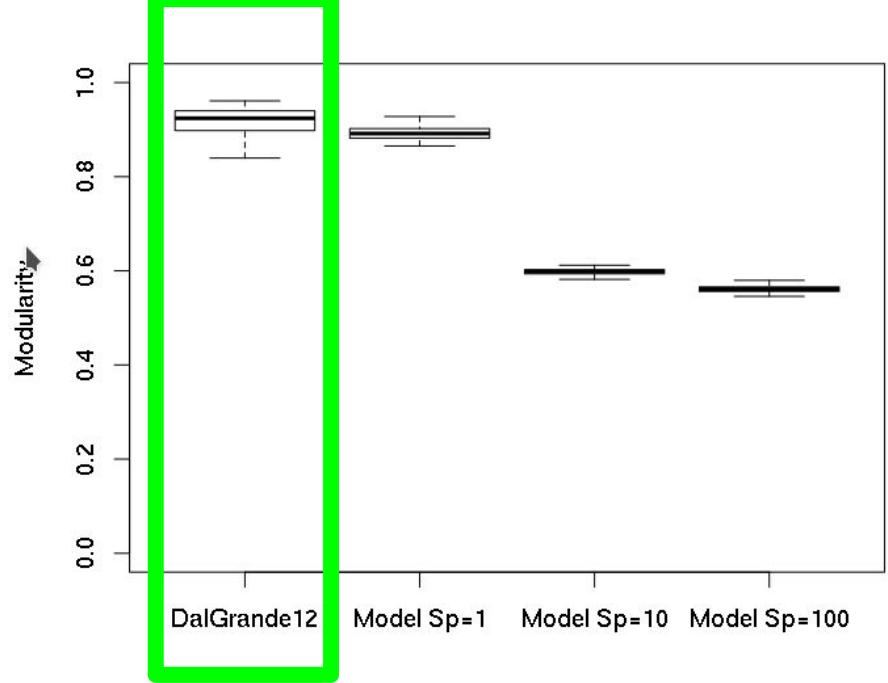
Barber MJ. 2007. Modularity and community detection in bipartite networks. Physical Review E, 76: 066102

Flores C, Poisot T, Valverde S Weitz J. 2016. BiMat: a MATLAB package to facilitate the analysis of bipartite networks. Methods in Ecology and Evolution, 7:127–132.

# Modularity



# Modularity



# Validation step

More quantitative comparison needed

=> Approximate Bayesian Computation, Beaumont 2010

- Check that the assumptions used to build the model are correct
- Confirm and refine observations made in other studies

# Future Experiments

Large scale study,

Speciation,

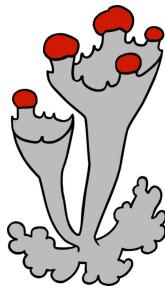
Emergence of Photobiont mediated guild,

....

# Thanks!



**Barcelona  
Supercomputing  
Center**  
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*British  
Lichen  
Society*



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BRITISH  
ECOLOGICAL  
SOCIETY

# Population Structure

Nodes Properties vs Spatial Structure:

**Betweenness centrality** (Martín González A, Dalsgaard, Olesen JM. 2010. Centrality measures and the importance of generalist species in pollination networks. Ecological Complexity 7, 36-43)

is the importance of a node as a connector between different parts of the network. Nodes with BC>0 connect areas of the network that would otherwise be sparsely or not connected at all. Species which are important to the cohesiveness of the network will have a positive BC.

**Betweenness centrality**

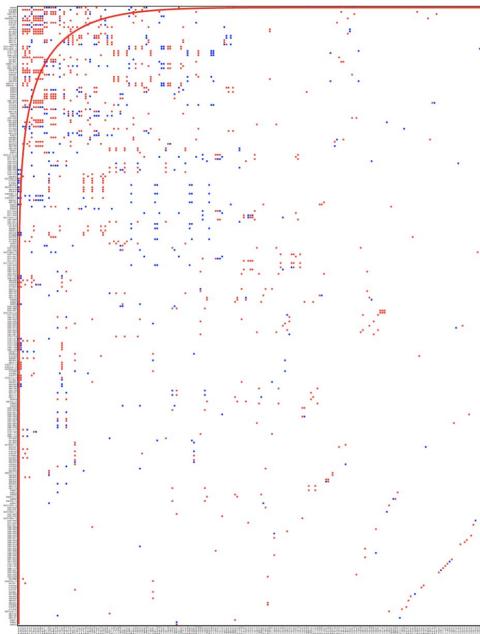
$$BC_i = 2 \sum_{j < k; i \neq j} \frac{g_{jk}(i)/g_{jk}}{(n - 1)(n - 2)}$$

n, number of species

$g_{jk}(i)$ , number of shortest paths between  $j$  and  $k$  going through  $i$

$g_{jk}$ , number of shortest paths linking  $j$  and  $k$

# Network metrics



## Nestedness

$$N_{NODF} = \frac{\sum_{ij} M_{ij}^{row} + \sum_{ij} M_{ij}^{col}}{\left[ \frac{m(m-1)}{2} \right] + \left[ \frac{n(n-1)}{2} \right]}$$

$$M_{ij}^{row} = \begin{cases} 0 & \text{if } k_i \leq k_j \\ n_{ij}/\min(k_i, k_j) & \text{otherwise} \end{cases}$$

$m, n$ , n° of rows and columns

$k_i$ , n° of interactions in row  $i$

$k_j$ , n° of interactions in row  $j$

$n_{ij}$ , n° of shared interactions between rows  $i$  and  $j$

Almeida-Neto M, Guimaraes P, Guimaraes PR Jr, Loyola RD, Ulrich W. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement Oikos, 117: 1227–1239

Flores C, Poisot T, Valverde S, Weitz J. 2016. BiMat: a MATLAB package to facilitate the analysis of bipartite networks. Methods in Ecology and Evolution, 7:127–132.

# Network metrics

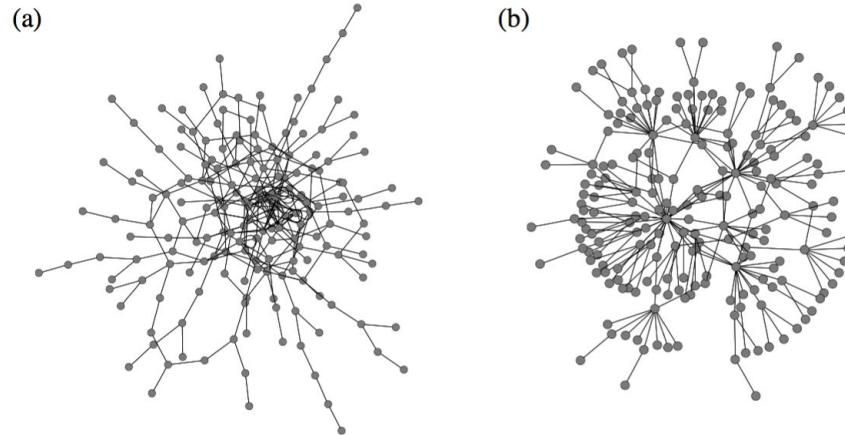
## Assortative/Disassortative mixing

$$r = \frac{M^{-1} \sum_i j_i k_i - [M^{-1} \sum_i \frac{1}{2}(j_i + k_i)]^2}{M^{-1} \sum_i \frac{1}{2}(j_i^2 + k_i^2) - [M^{-1} \sum_i \frac{1}{2}(j_i + k_i)]^2}$$

$j_i, k_i$  degrees of the vertices at the ends of  $i$ th edge, with  $i = 1, \dots, M$

# Network metrics

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Newman M.E.J. 2002. Assortative Mixing in Networks. Phys. Rev. Lett. 89, 208701

Newman, M.E.J and Girvan M. Mixing patterns and community structure in networks. Statistical Mechanics of Complex Networks, n° 625 Lecture Notes in Physics, pp. 66-87, Springer, Berlin (2003)

# Network metrics

## Asymmetry metrics

$$d_{ij}^F = \frac{w_{ij}}{\sum_j w_{ij}}$$

$$d_{ji}^A = \frac{w_{ji}}{\sum_i w_{ji}}$$

$$AS(i, j) = \frac{d_{ij}^F - d_{ji}^A}{\max(d_{ij}^F, d_{ji}^A)}$$

$d_{ij}^F$ , dependence of fungi species  $i$  on algae species  $j$

$d_{ji}^A$ , dependence of algae species  $j$  on fungi species  $i$

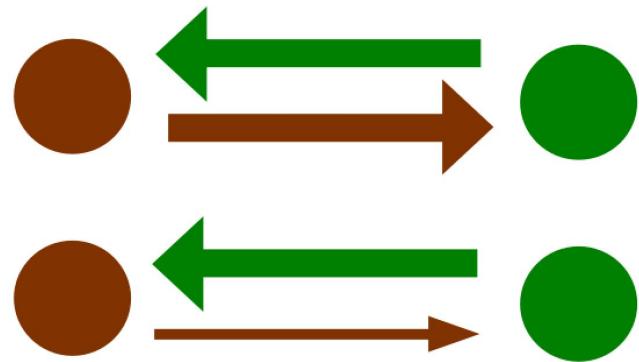
# Network metrics

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# Network metrics

## Modularity (Barber MJ. 2007. Modularity and community detection in bipartite networks. Physical Review E, 76: 066102)

### MODULARITY:

Modularity indicates the presence of dense clusters of nodes with many overlapping interactions embedded within the network. Clusters are considered dense when they have high internal edge density relative to the expected edge density in the null model. These dense clusters are termed modules. Identifying modules and estimating the associated modularity require a partitioning of the network.

# Network metrics

## Modularity

$$Q_R = \frac{W}{E}$$

$E$ , edges in a network

$W$ , n° of edges established between  
members of the same module

Poisot T. 2013. An a posteriori measure of network modularity. F1000 Research, 2:130

Flores C, Poisot T, Valverde S Weitz J. 2016. BiMat: a MATLAB package to facilitate the analysis of bipartite networks. Methods in Ecology and Evolution, 7:127–132.

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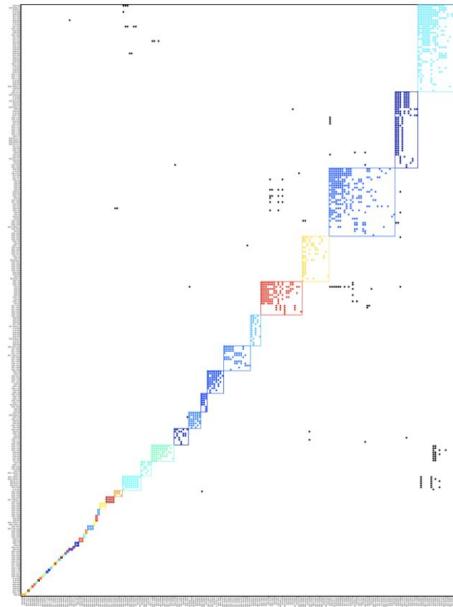
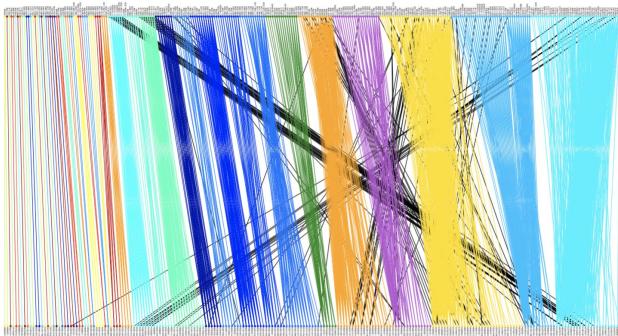
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# Population Structure

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# Exploration of the model dynamics

