

El potencial de la genética en el estudio de la  
biodiversidad: El caso del liquen *Bryoria*.

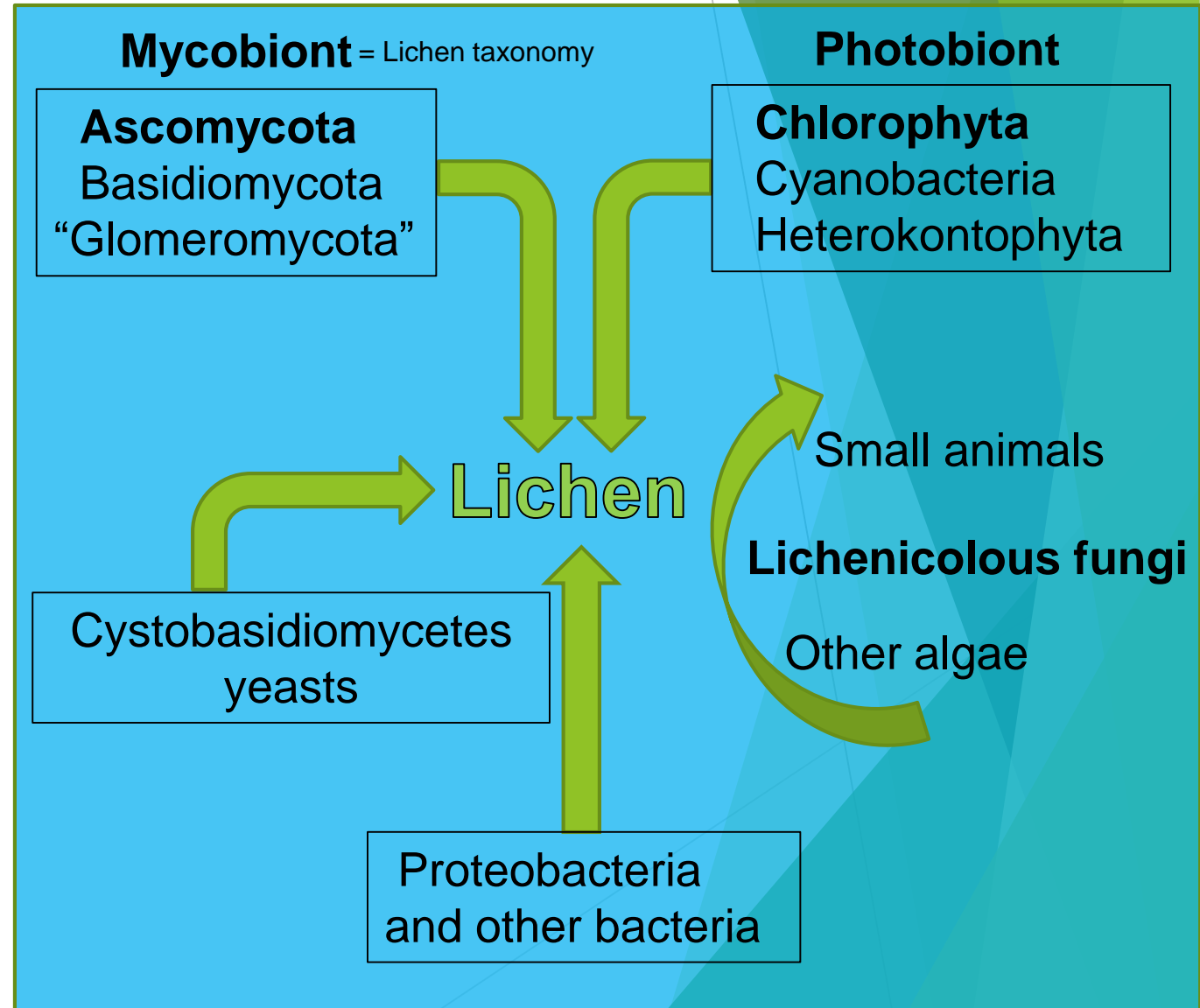
*Carlos Galán Boluda*

*Facultad de Ciencias Forestales, UANL, Linares, México, 23-01-2019*

# Introduction



Tundra community, Norway



# Introduction



**Crustose**



**Foliose**



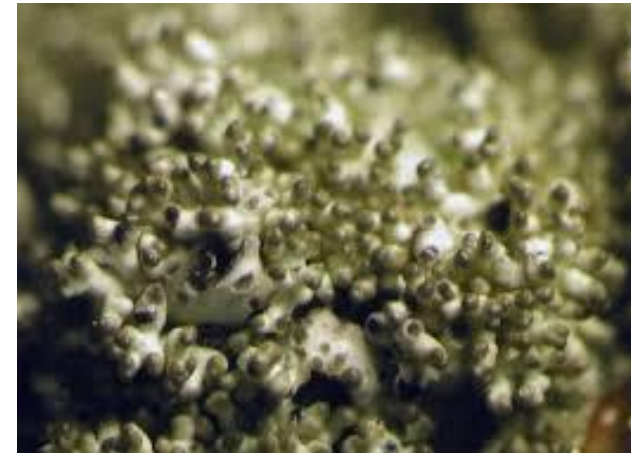
**Fruticose**



**Apothecia**



**Soralia**



**Isidia**

# Introduction



Dikarya



At least 16 independent origins of lichenized fungi

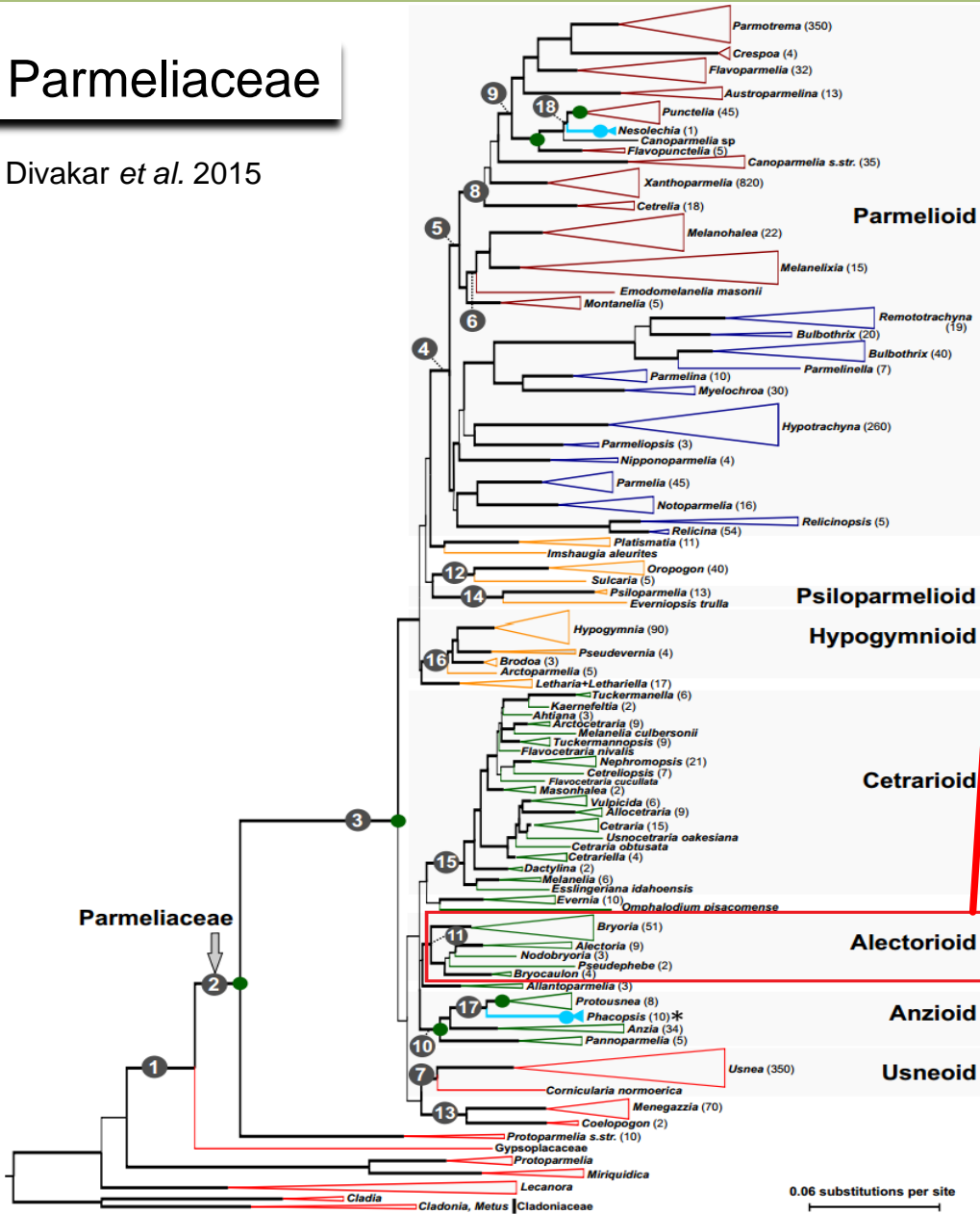
Lecanoromycetes

*Usnea trichodeoides*, Tanzania

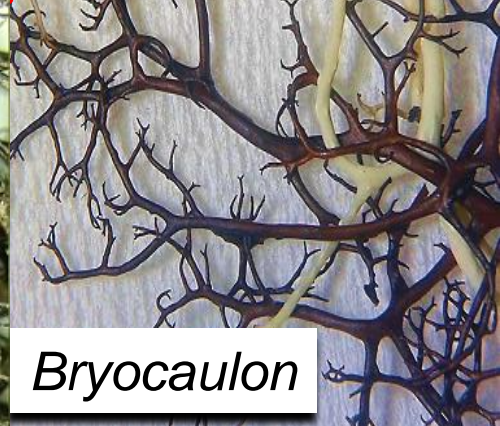
# Introduction

## Parmeliaceae

Divakar *et al.* 2015



## Alectorioid



# Introduction

Example of three sampled regions



Norway



Norway



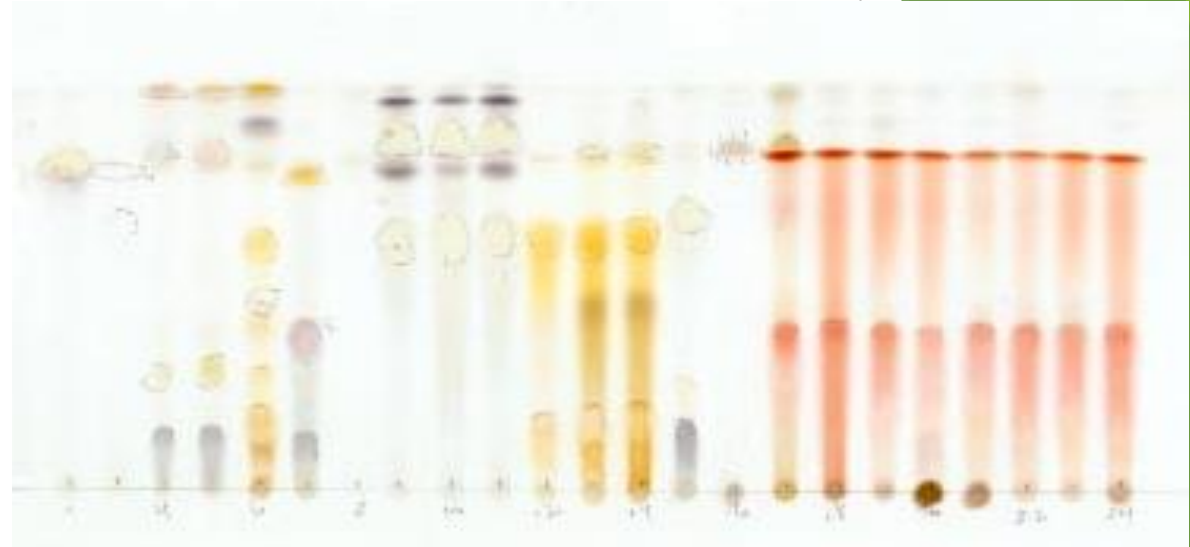
Portugal

# Introduction

**Extrolite:** extracellular crystals of secondary metabolites produced by the fungus.



**Spot test**



**TLC**

**No Usnic acid**



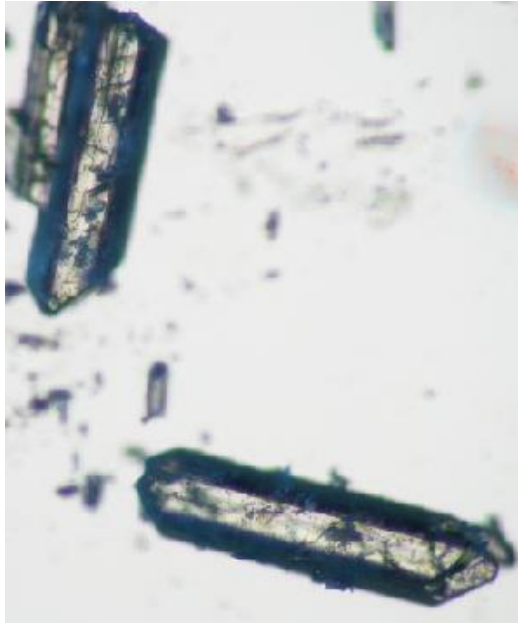
**Usnic acid**



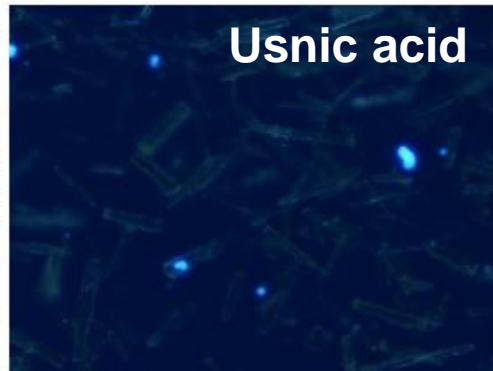
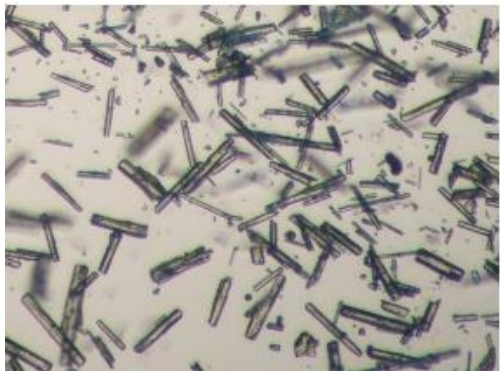
# Introduction

**Extrolite:** extracellular crystals of secondary metabolites produced by the fungus.

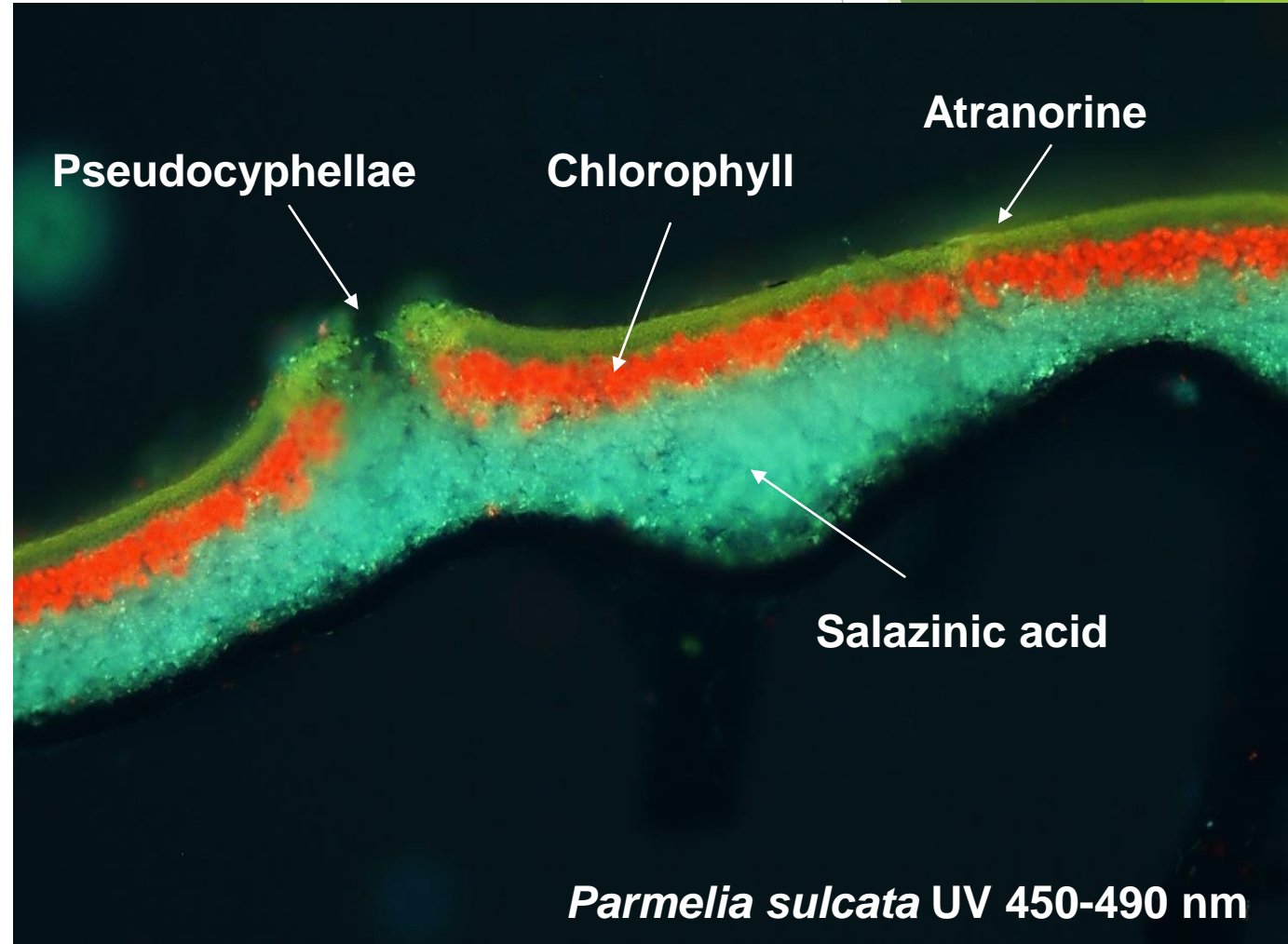
White light



UV 450-490 nm

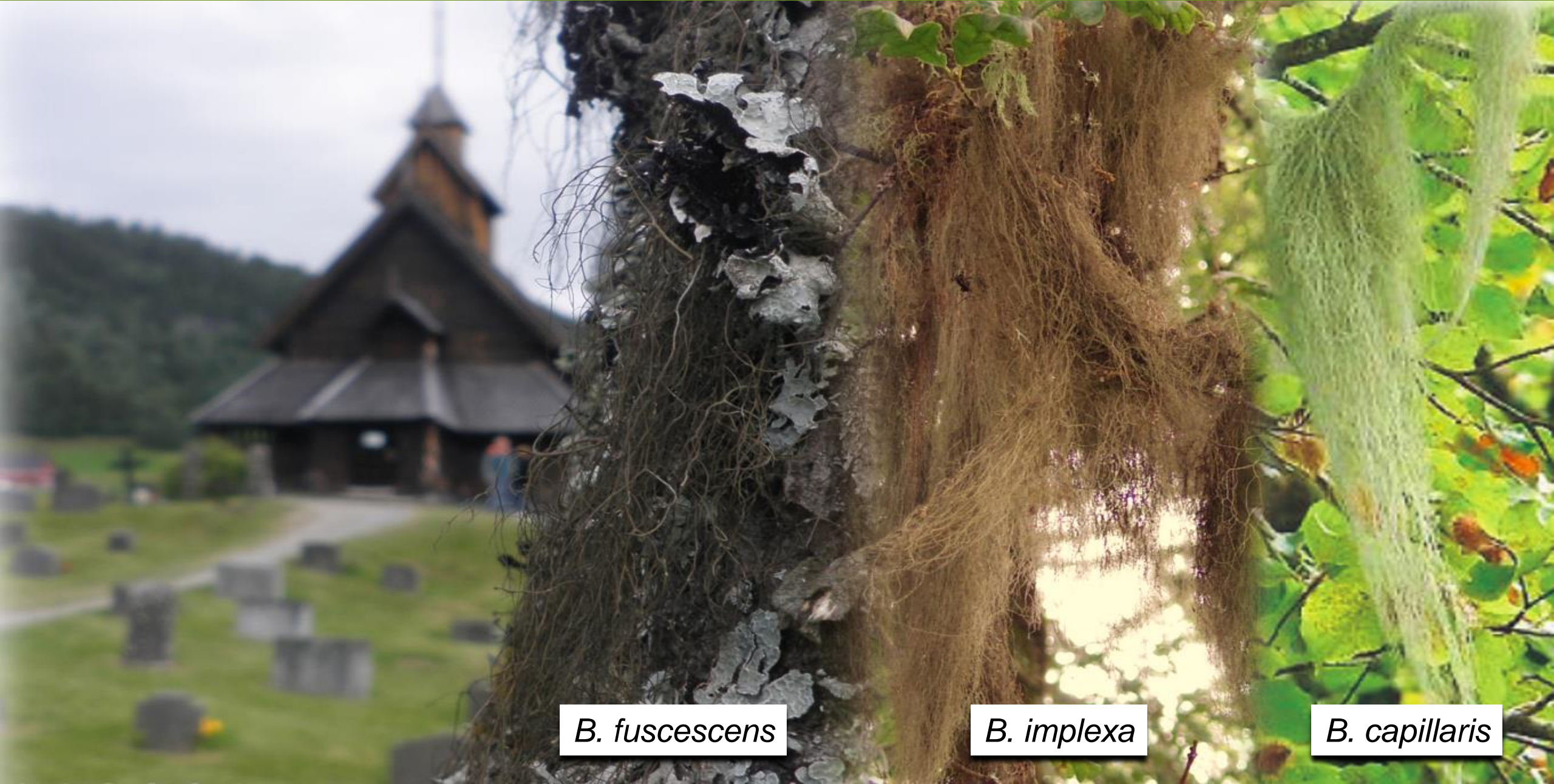


UV 450-490 nm





# Introduction



*B. fuscescens*

*B. implexa*

*B. capillaris*

# Introduction



## Main key characters:

- Extrolites
- Soralia
- Pseudocyphellae
- Thallus colour
- Branching angles

**Tabla 2.** Sustancias químicas diagnóstico que junto con caracteres adicionales permiten distinguir las especies de *Bryoria* sect. *Implexae*. Los caracteres adicionales incluyen la coloración del talo, los ángulos de ramificación, las características de los soralios y pseudocifelas y la distribución.

<b>Especie</b>	<b>Sustancia diagnóstico</b>
<i>Bryoria austromontana</i>	Ácido fumarprotocetrárico
<i>B. capillaris</i>	Ácido barbatólico
<i>B. friabilis</i>	Ácido girofórico
<i>B. fuscescens</i>	Ácido fumarprotocetrárico
<i>B. glabra</i>	Ácido fumarprotocetrárico
<i>B. implexa</i>	Ácido psorómico
<i>B. inactiva</i>	Sin sustancias
<i>B. kockiana</i>	Ácido psorómico
<i>B. pikei</i>	Ácido barbatólico
<i>B. pseudofuscescens</i>	Ácido norestítico
<i>B. salazinica</i>	Ácido salazínico
<i>B. vrangiana</i>	Ácido fumarprotocetrárico

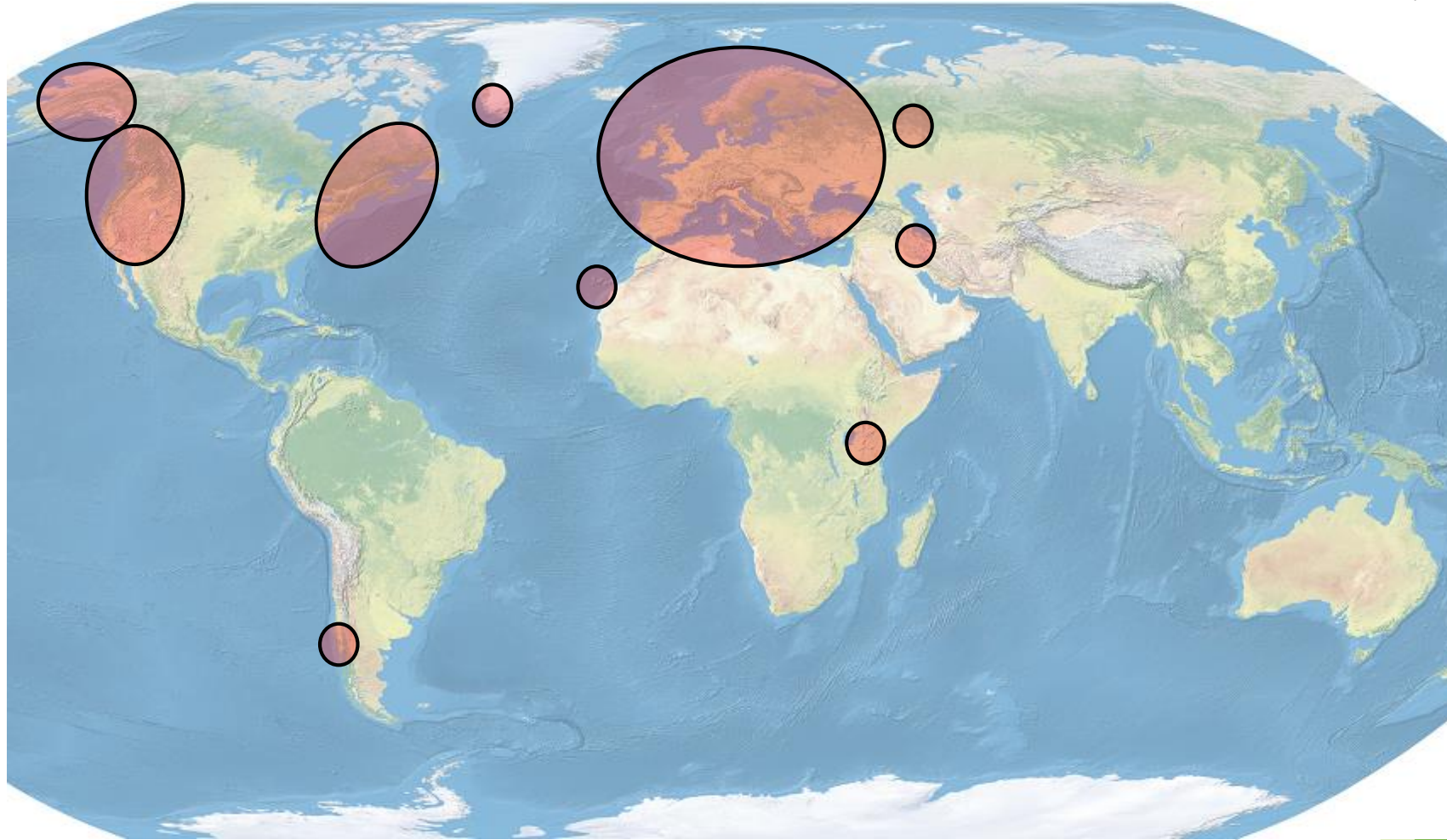
# Main questions

- How many species contain *Bryoria* section *Implexae*?
- How the environment affects the biology of *Bryoria* sect. *Implexae*?
- How *Bryoria* sect. *Implexae* has been affected by the last glacial period?



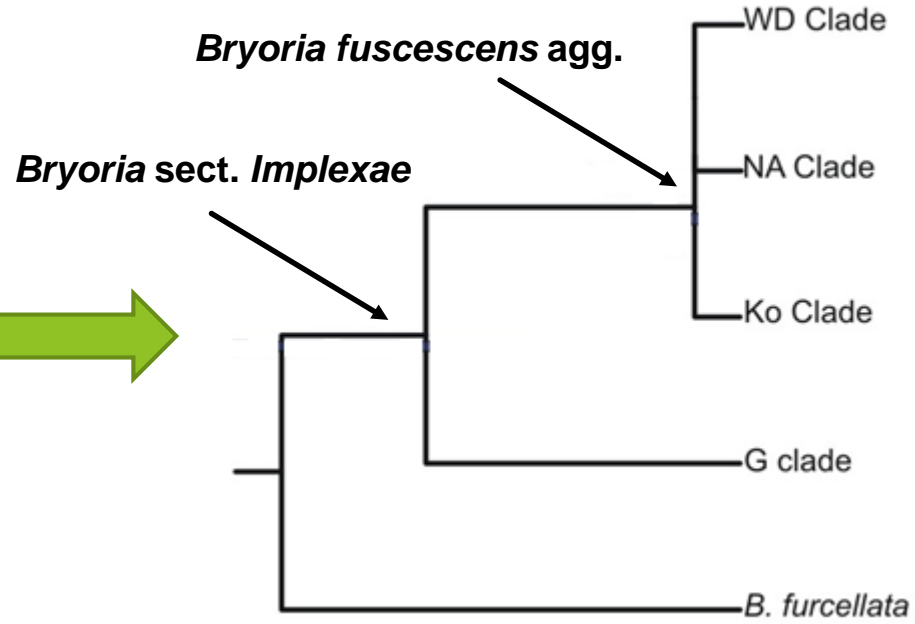
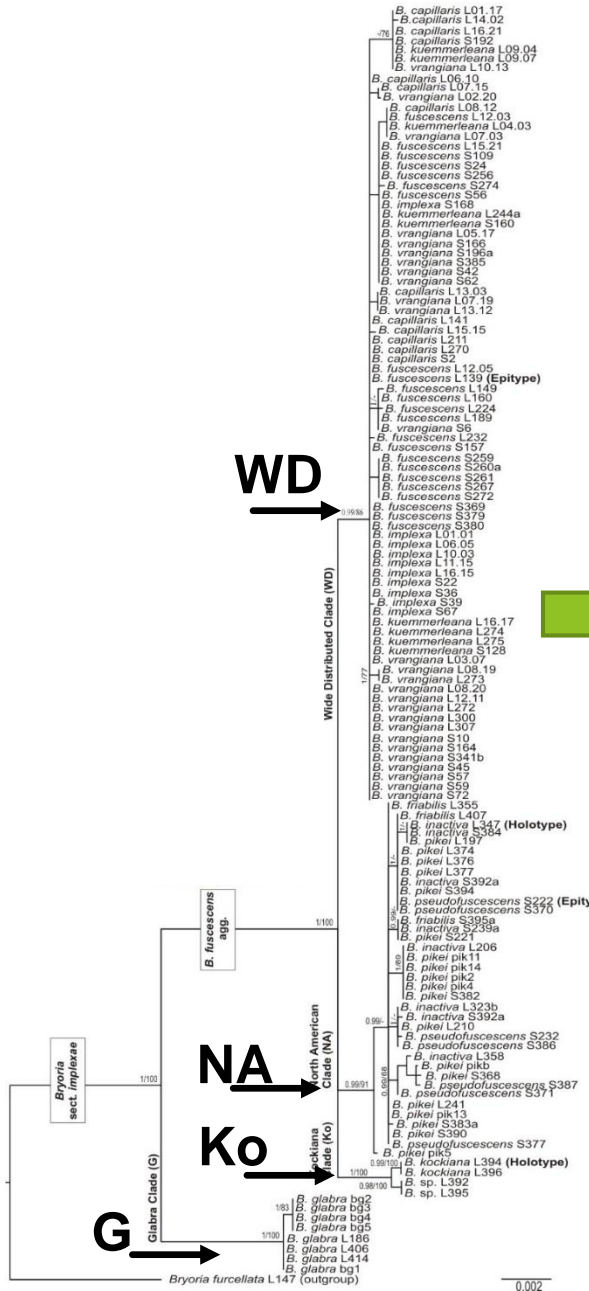
# Materials and methods

Approximately 2.100 specimens



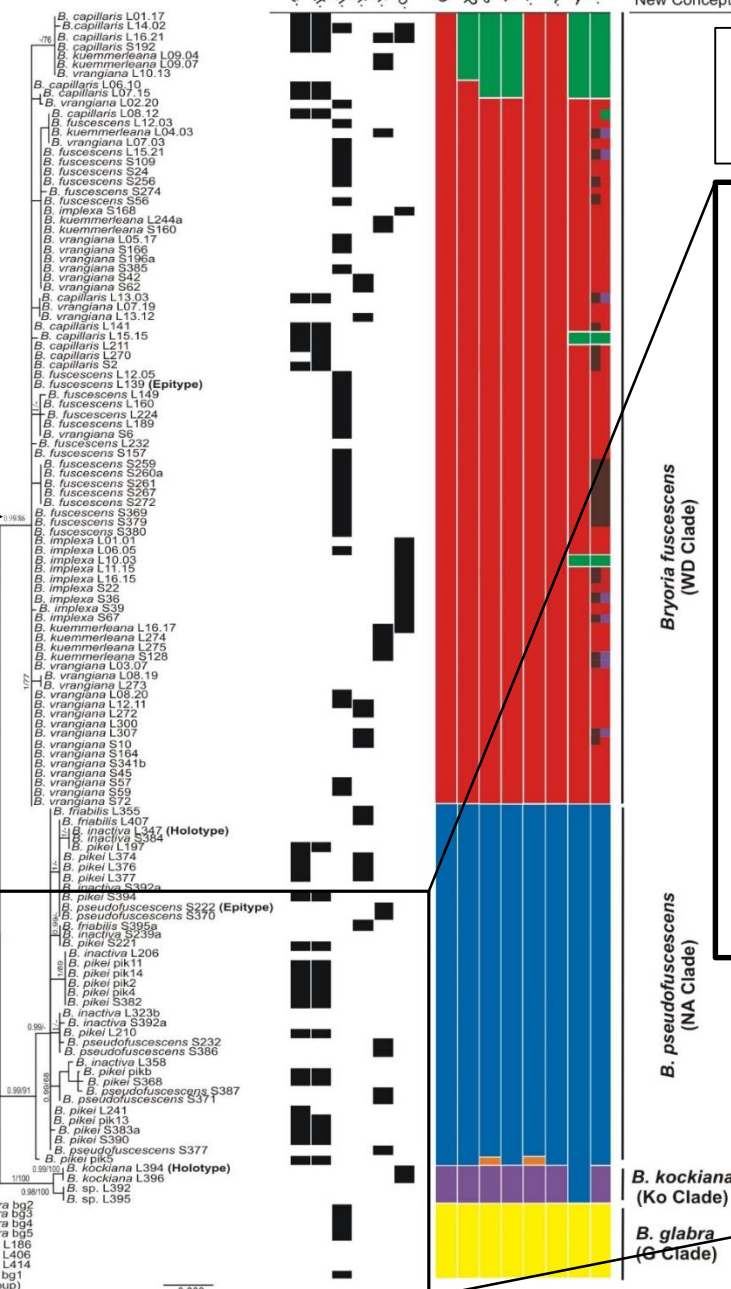
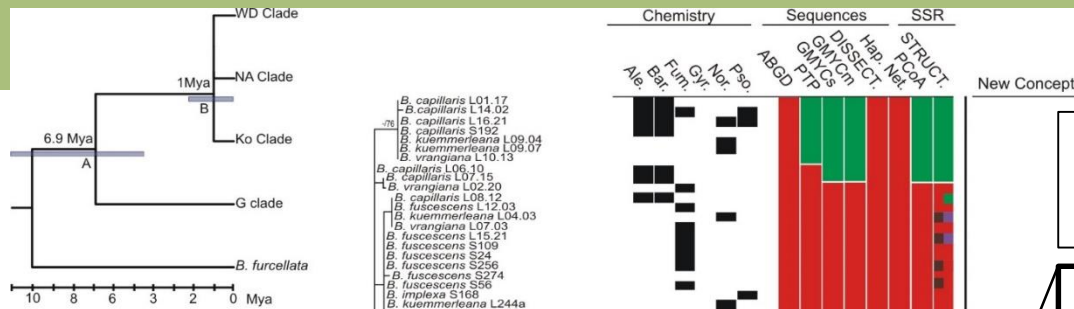
# Taxonomical results

ML and Bayesian tree form the concatenated matrix (ITS, IGS & GAPDH)

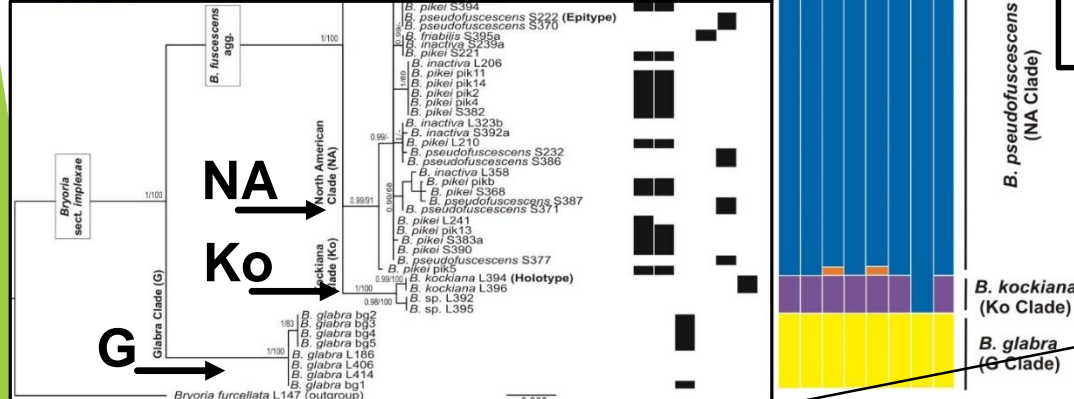
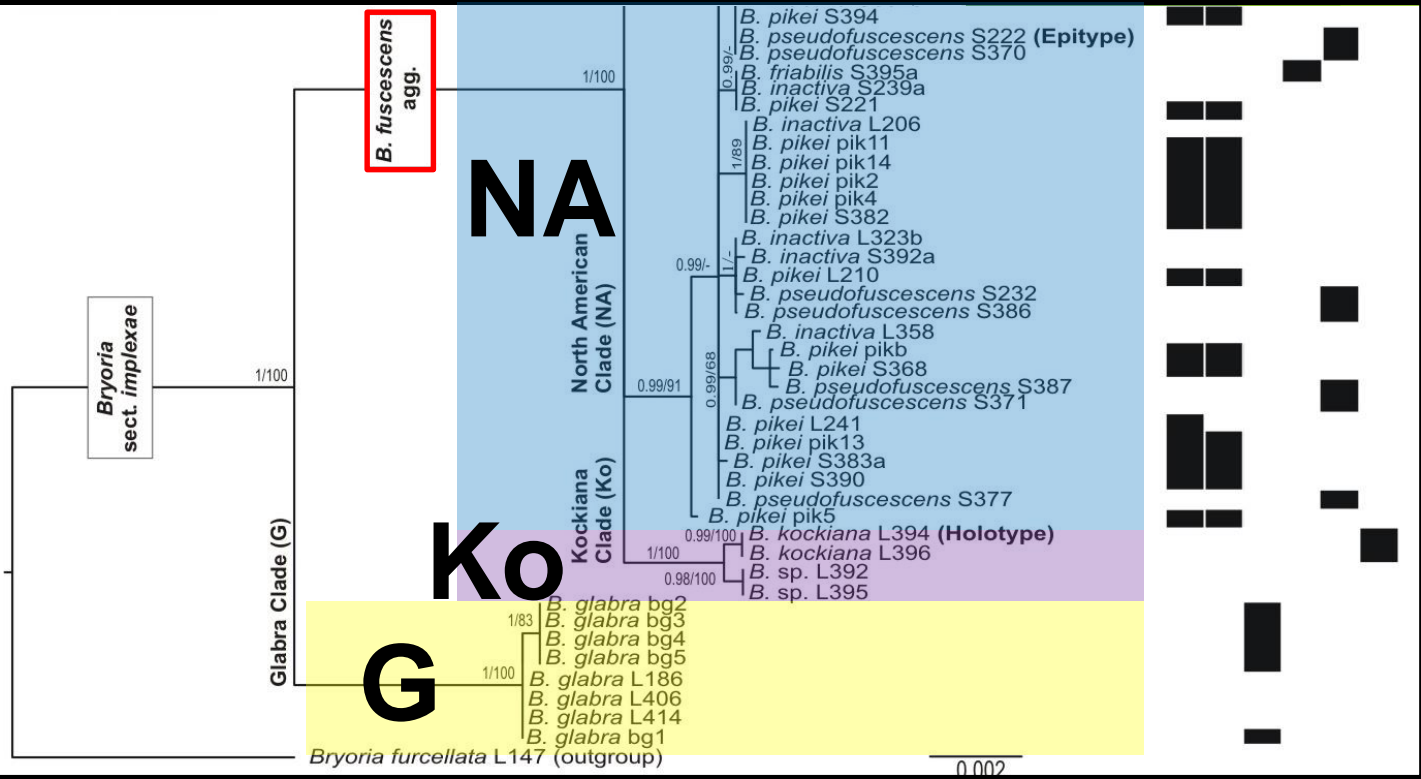


Tree backbone well supported

# Taxonomical results

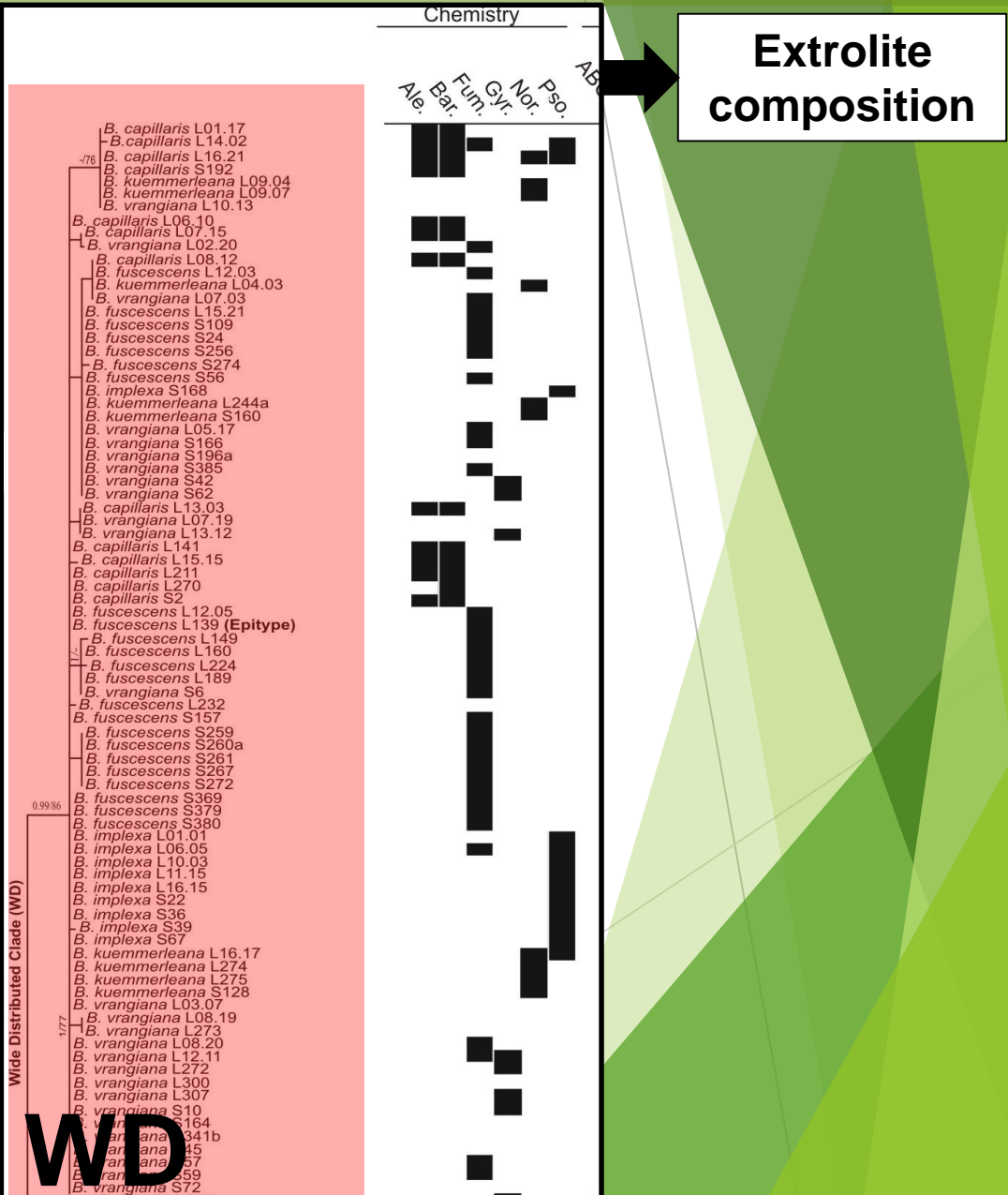
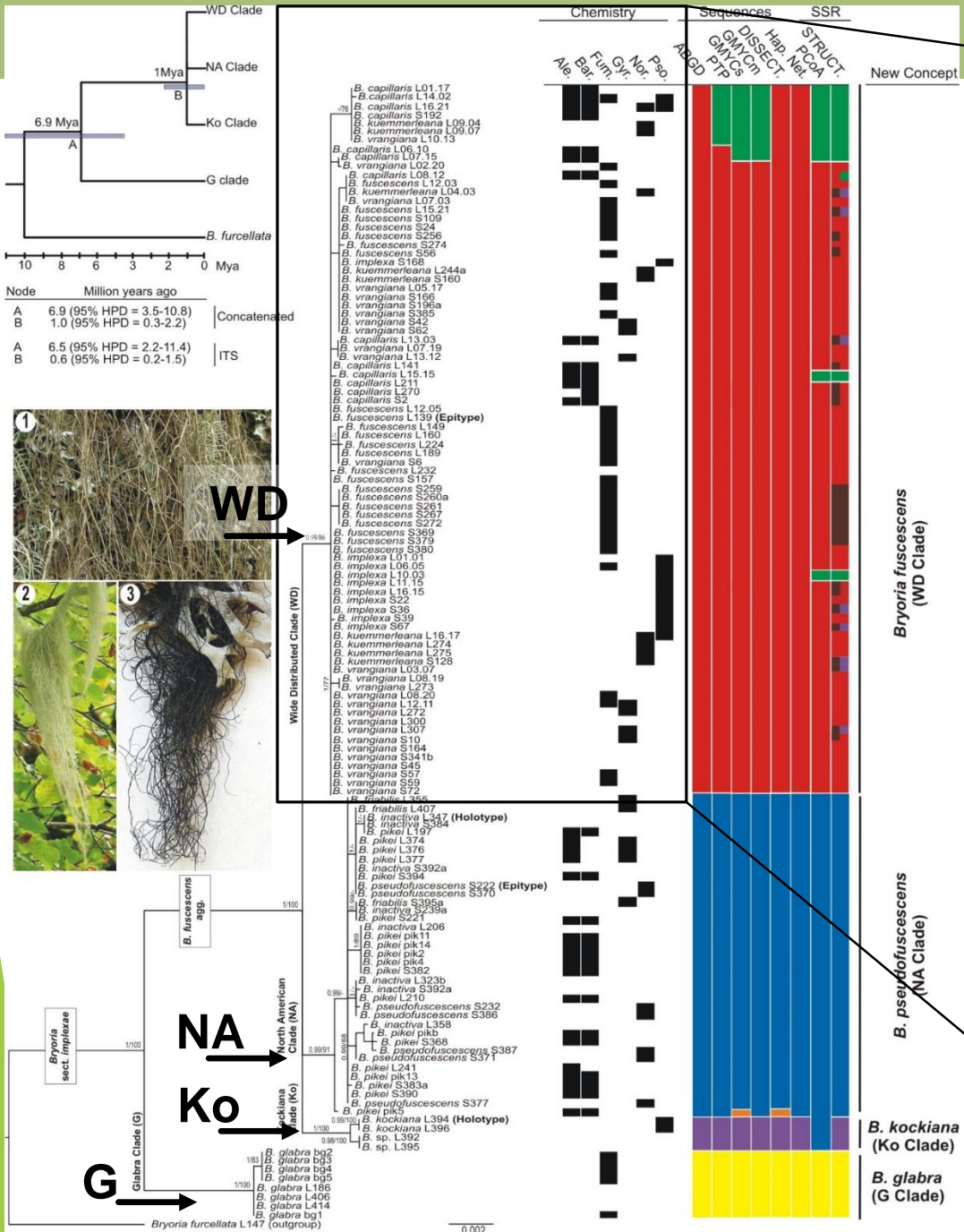


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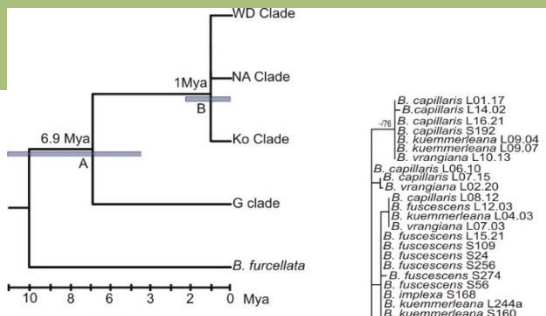


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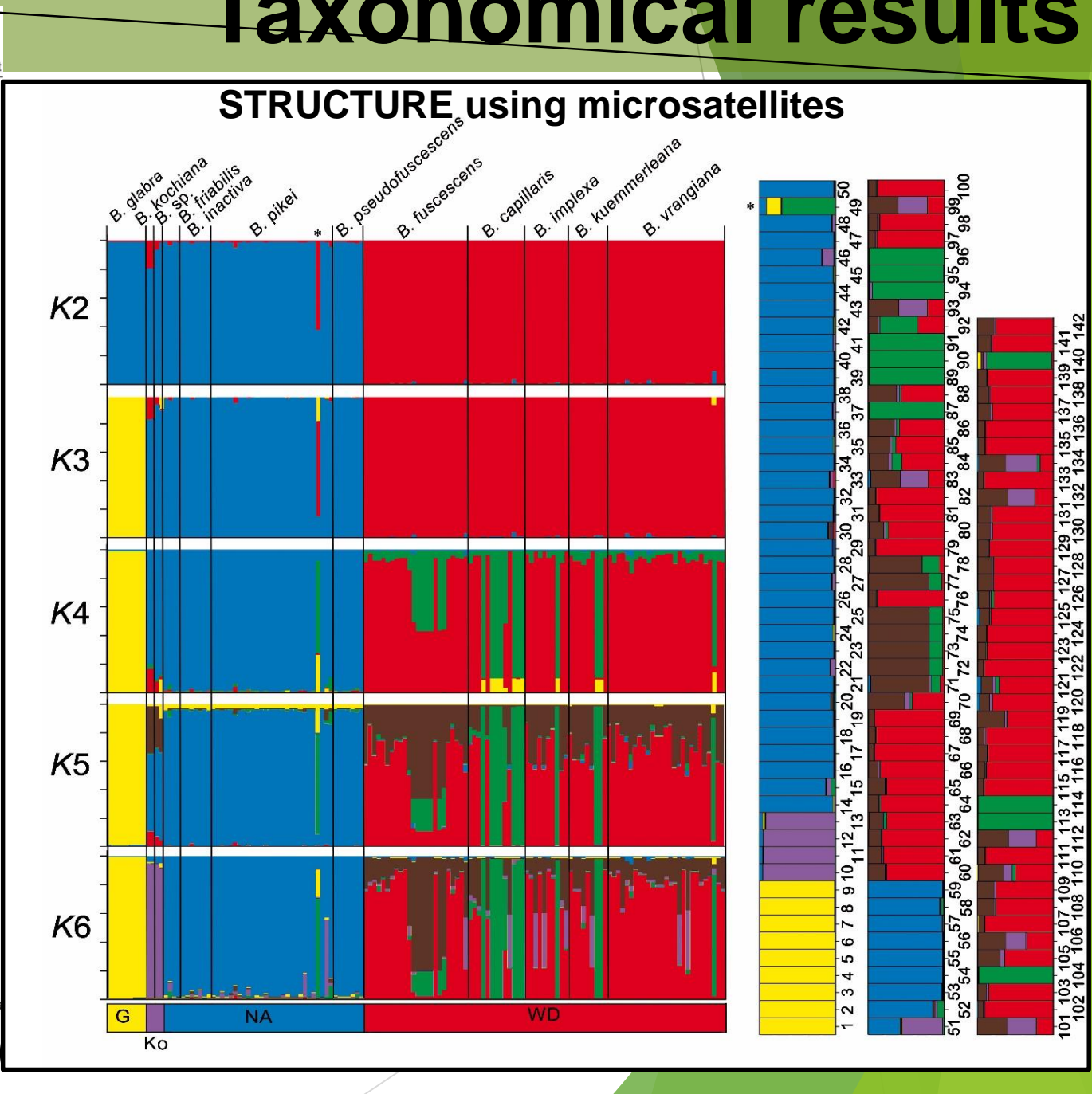
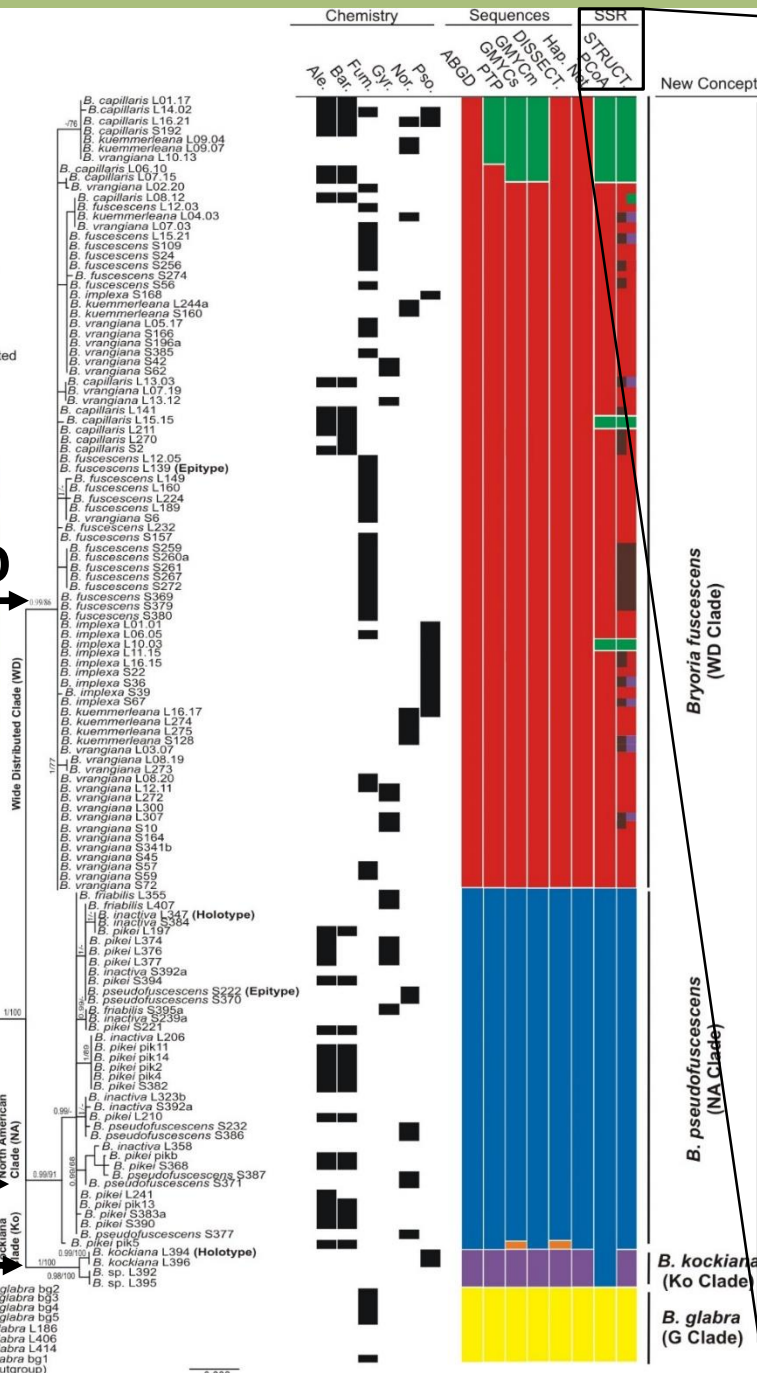
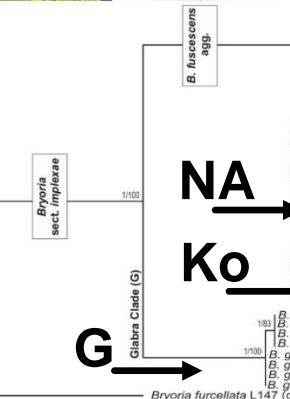
# Taxonomical results



# Taxonomical results

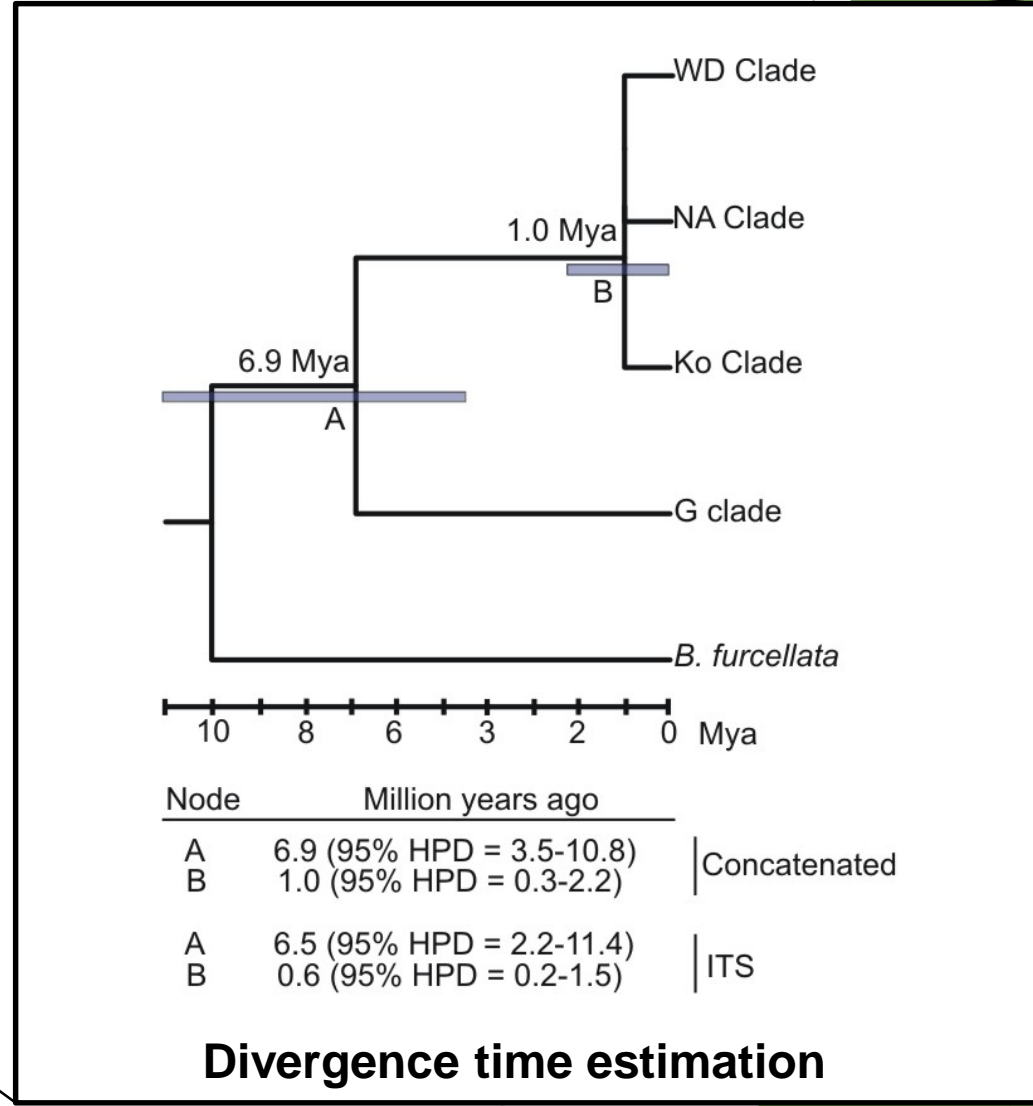
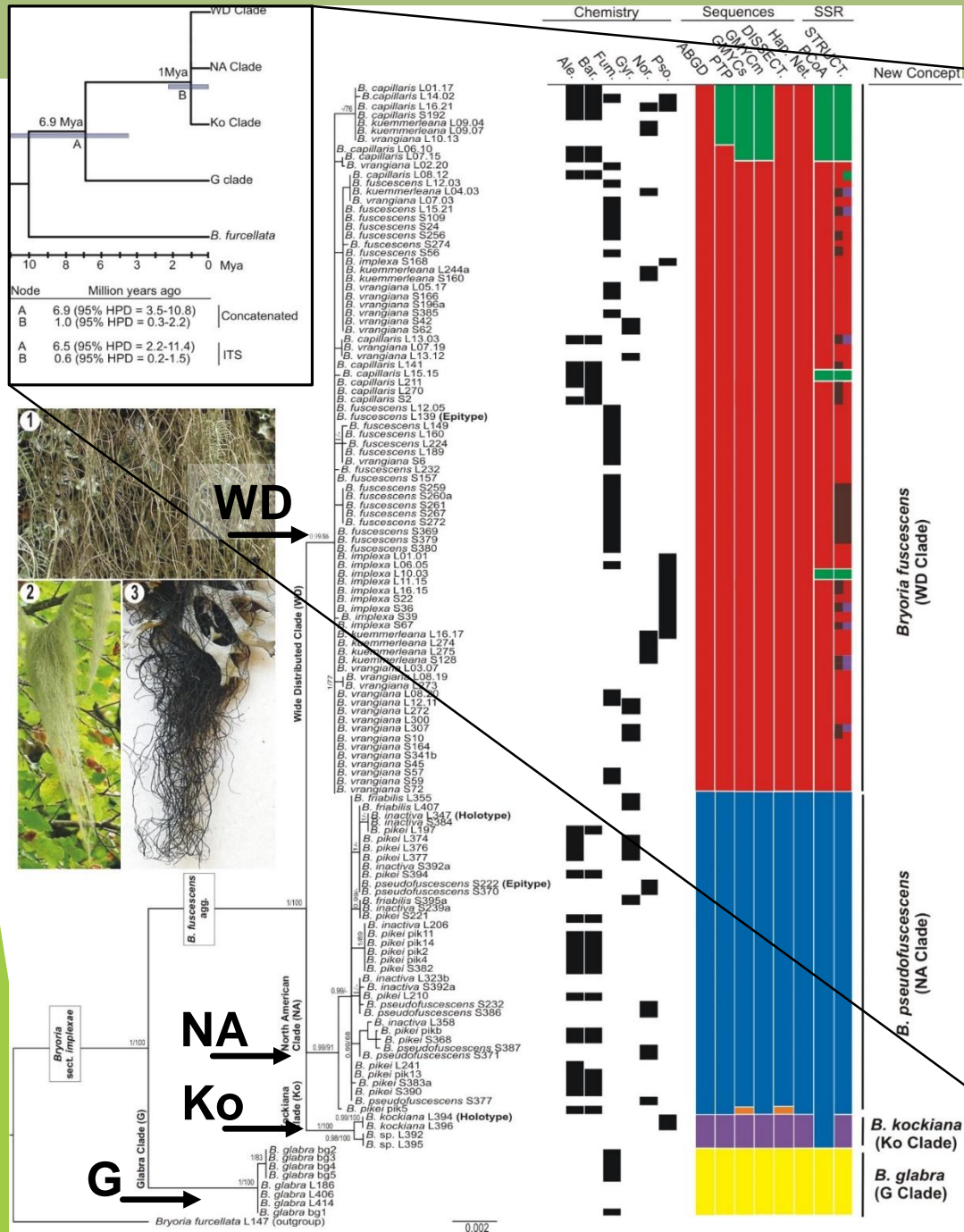


Node	Million years ago	Method
A	6.9 (95% HPD = 3.5-10.8)	Concatenated
B	1.0 (95% HPD = 0.3-2.2)	
A	6.5 (95% HPD = 2.2-11.4)	ITS
B	0.6 (95% HPD = 0.2-1.5)	





# Taxonomical results



**WD**

**NA**

**Ko**

**G**

# Taxonomical results

## Proposed species concept

*Bryoria fuscescens*

Syn: *B. capillaris*, *B. implexa*, *B. kuemmerleana*, *B. vrangiana*.

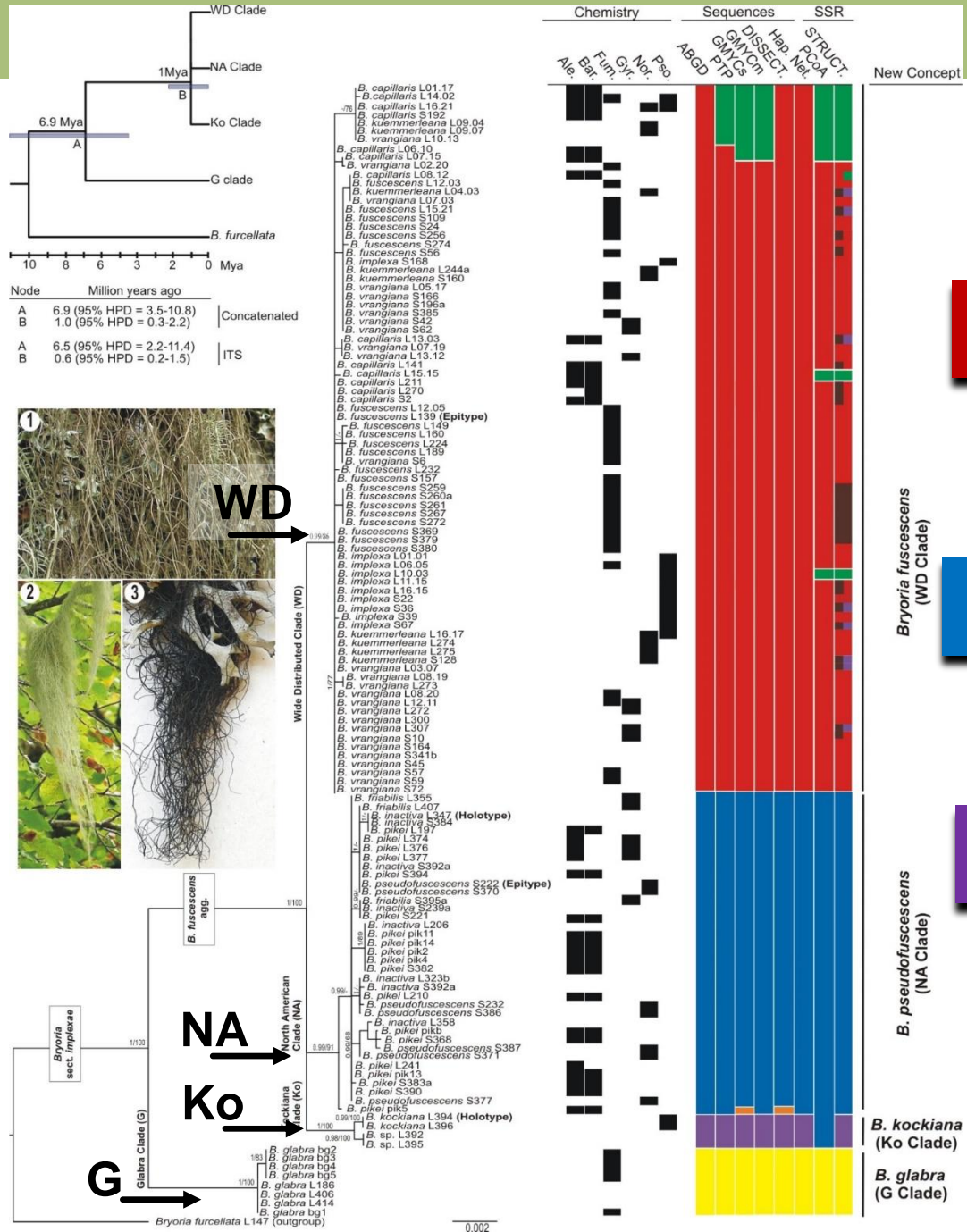
*Bryoria pseudofuscescens*

Syn: *B. friabilis*, *B. inactiva*, *B. pikei*.

*Bryoria kockiana*

Syn: *B. sp.*

*Bryoria glabra*

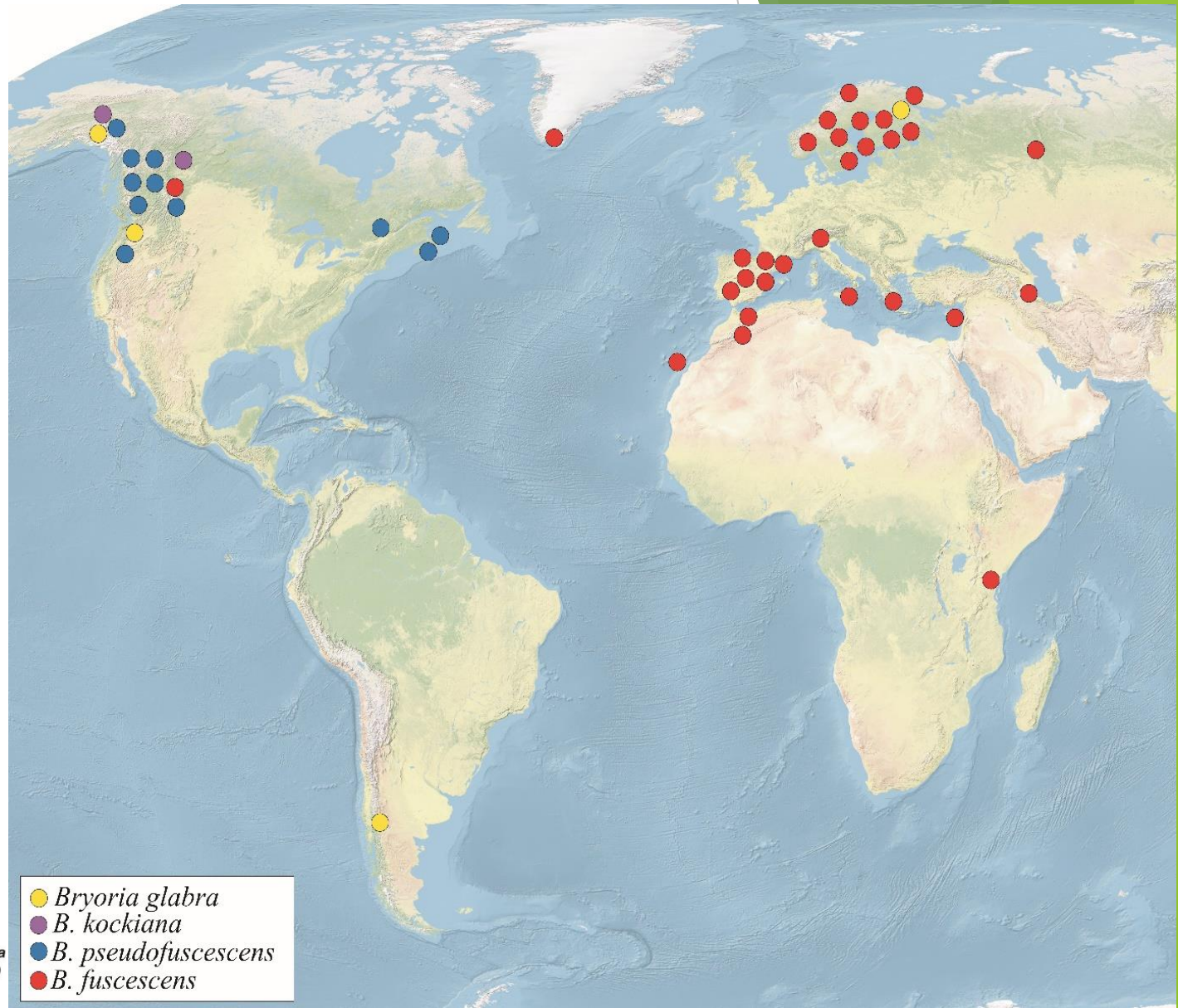
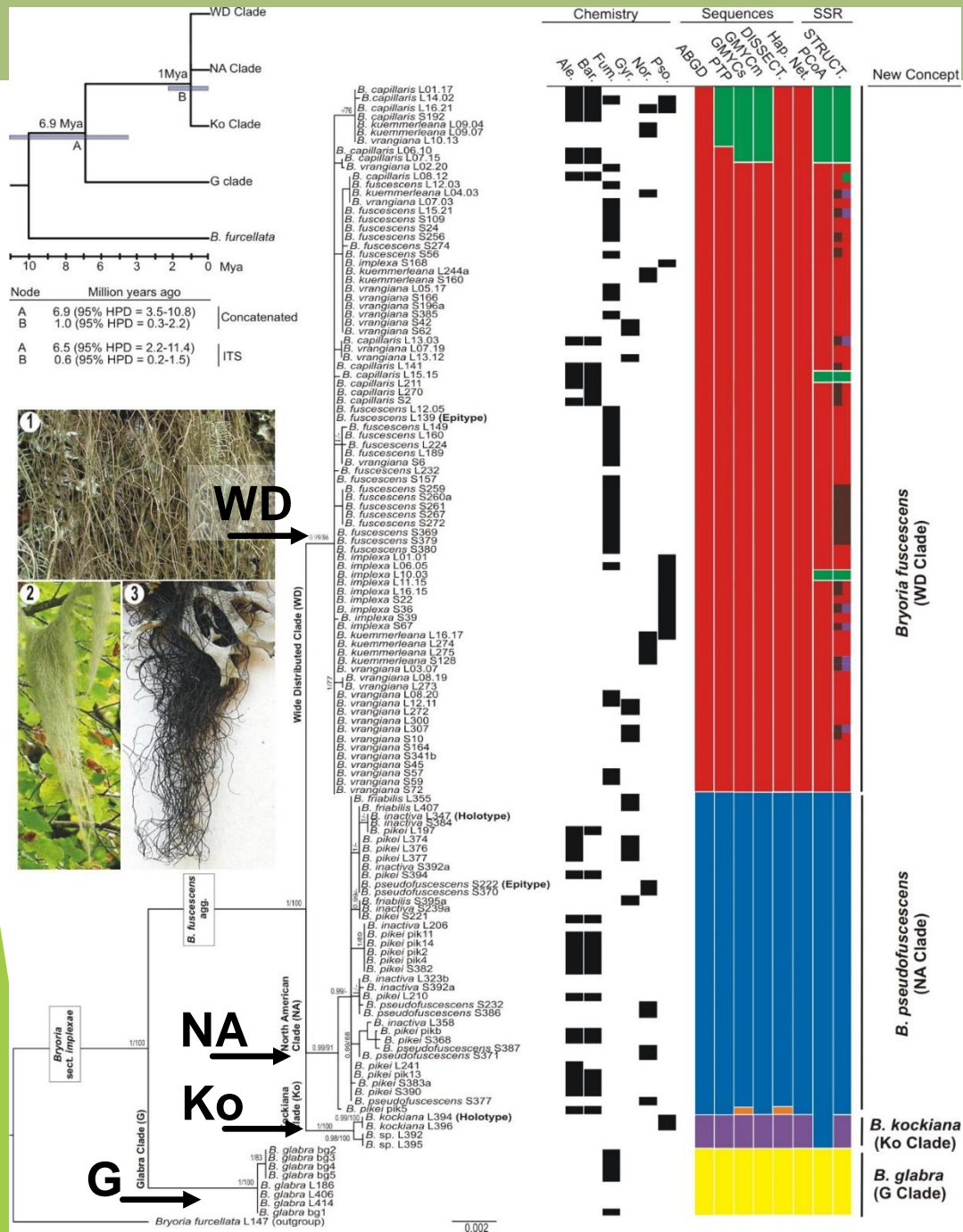


*Bryoria fuscescens*  
(WD Clade)

*B. pseudofuscescens*  
(NA Clade)

*B. kockiana*  
(Ko Clade)  
*B. glabra*  
(G Clade)

# Taxonomical results



# Population genetics in *Bryoria fuscescens*

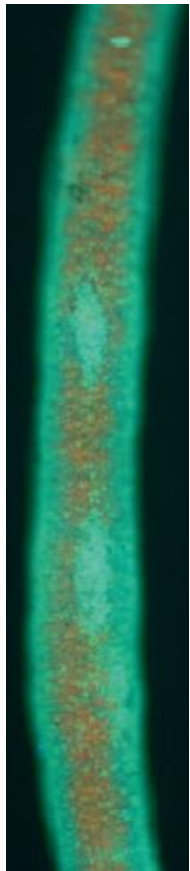
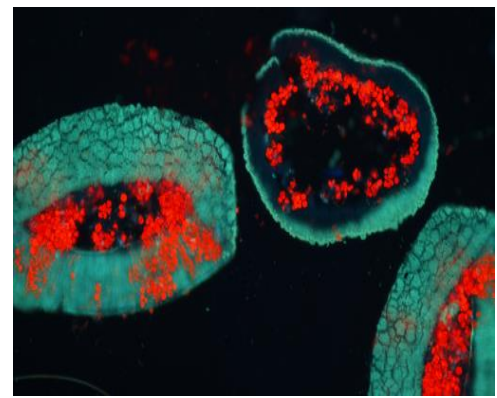
## Phenotype-capillaris

- Usually pale
- With barbatolic acid
- Soralia rare
- Angles usually acute

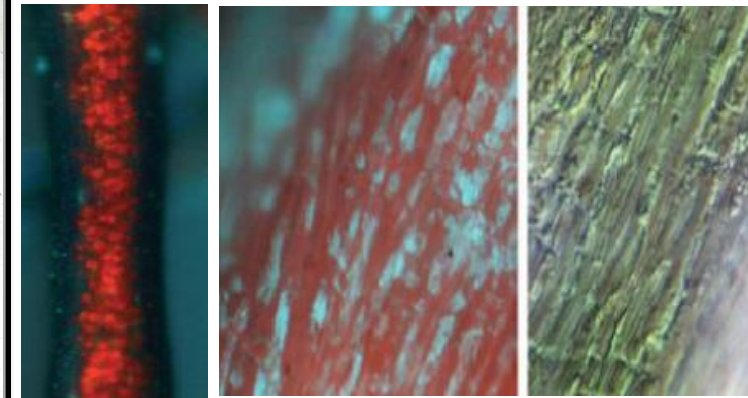
## *Bryoria fuscescens* s. str.

## Phenotype-fuscescens

- Usually dark
- Without barbatolic acid
- Soralia frequent
- Angles variable

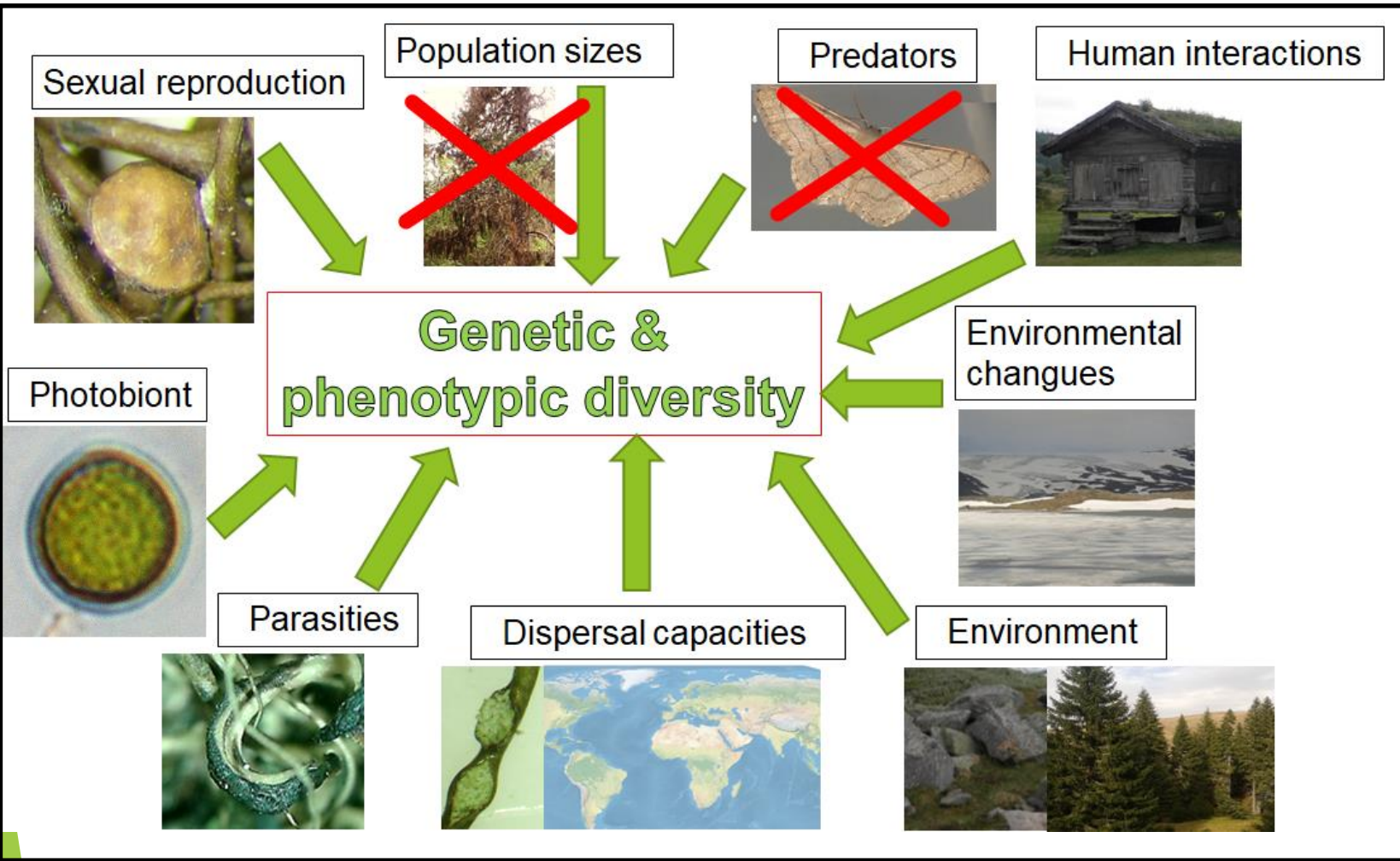


Cortical UV autofluorescence



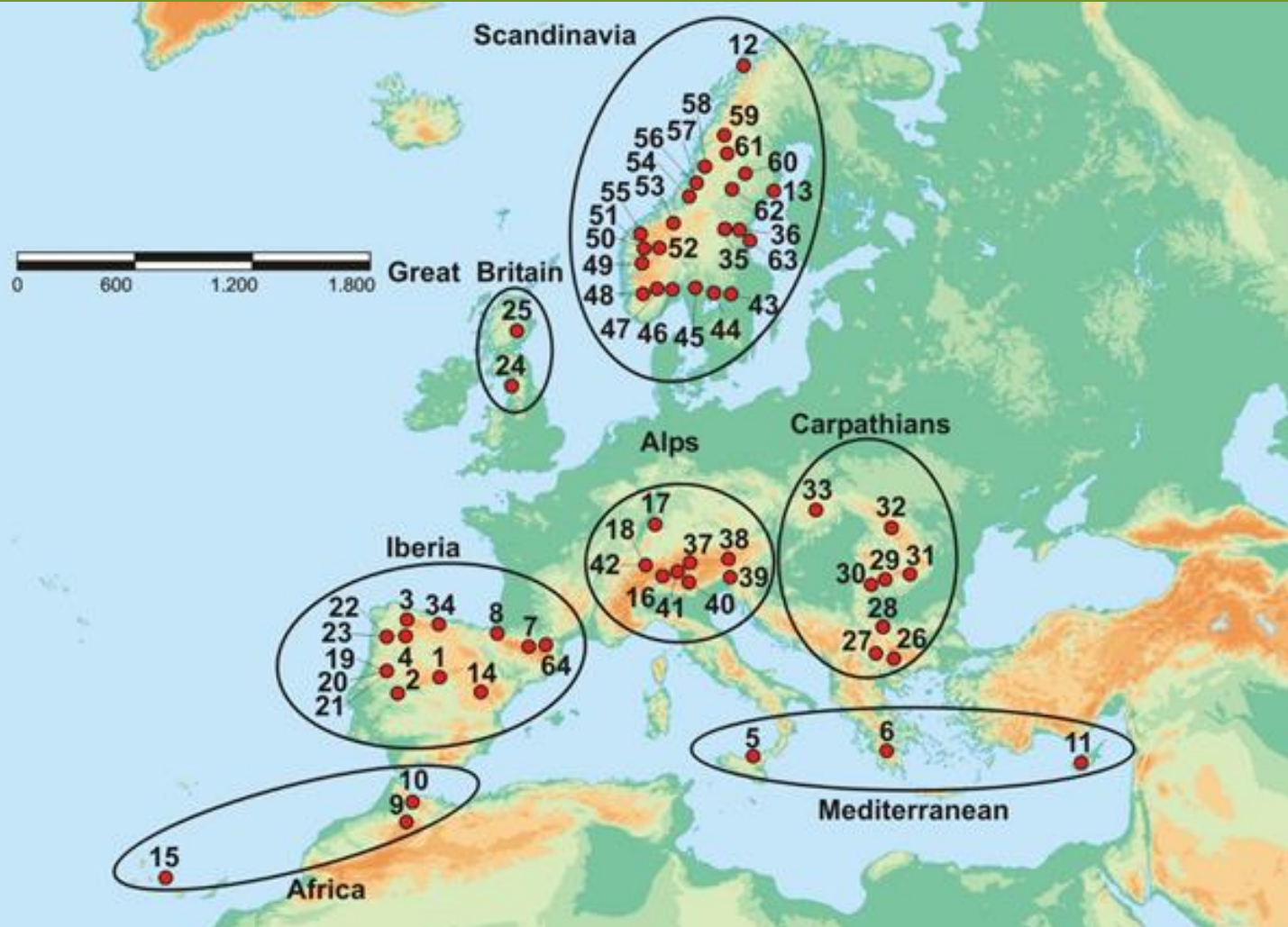
Cortical UV autofluorescence

# Population genetics in *Bryoria fuscescens*



***Bryoria* morphospecies growing together** →  
What is producing that phenotypes?

# Population genetics in *Bryoria fuscescens*



**Table 1.** Amplified and analysed SSRs. Left: Number of specimens with successful amplification for each locus, and its respective number of alleles. Right: Selected loci and specimens for the analyses after remove unexpected alleles and specimens with missing data.

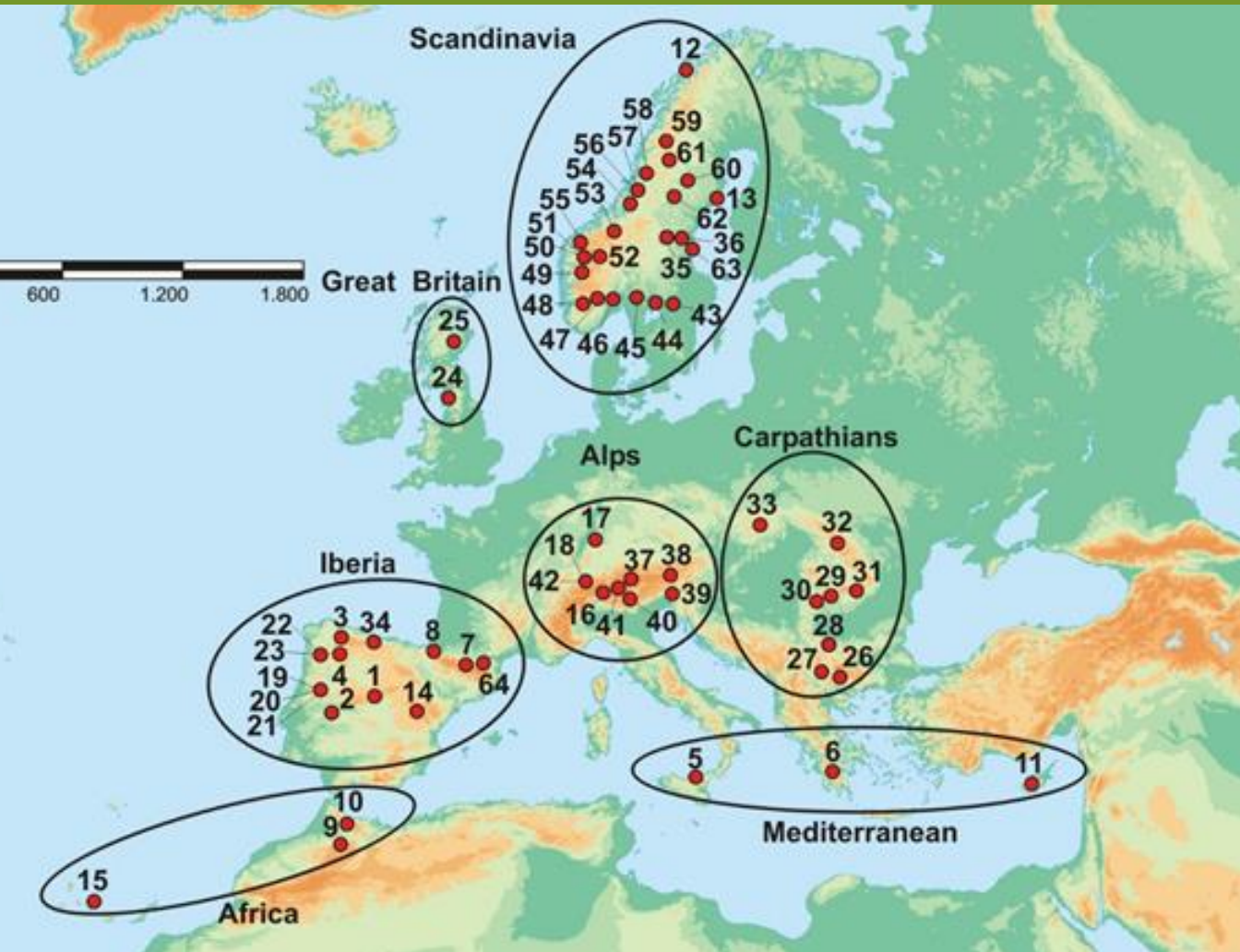
Locus	Amplified SSRs		SSRs used for the analyses	
	Specimens	Alleles	Specimens	Alleles
Bi01	1384	22	Not used	Not used
Bi02	1123	6	Not used	Not used
Bi03	1391	5	1359	5
Bi04	1388	8	1359	7
Bi05	1359	14	1359	10
Bi06	1366	22	1359	21
Bi07	1368	6	1359	6
Bi08	1385	5	1359	5
Bi09	597	3	Not used	Not used
Bi10	1393	5	1359	3
Bi11	1391	12	1359	10
Bi12	1399	22	1359	21
Bi13	1359	18	1359	18
Bi14	1391	4	1359	3
Bi15	1071	3	Not used	Not used
Bi16	1360	6	1359	6
Bi18	1359	9	1359	9
Bi19	1388	8	1359	6

1.400 specimens, 64 populations, 18 microsatellites

35 specimens used for a phylogenetical reconstruction  
(3 standard loci, and 5 new loci)

1.359 specimens  
14 microsatellites  
No missing data

# Population genetics in *Bryoria fuscescens*



**Table S6.** Global Analysis of Molecular Variance (AMOVA) using 14 loci, 1359 individuals, 64 populations and the 7 geographical regions from Fig. 1.  $F_{SC} = 0.21381$ ,  $F_{ST} = 0.23187$  and  $F_{CT} = 0.02297$ , statistically significant with  $P \leq 0.035$ .

Source of variation	df	Sum of squares	Variance components	% of variation
Among regions	6	211.80	0.089	2.30
Among populations within regions	57	1146.23	0.808	20.89
Within populations	1295	3846.72	2.970	76.81
<b>Total</b>	<b>1358</b>	<b>5204.75</b>	<b>3.867</b>	

## AMOVA

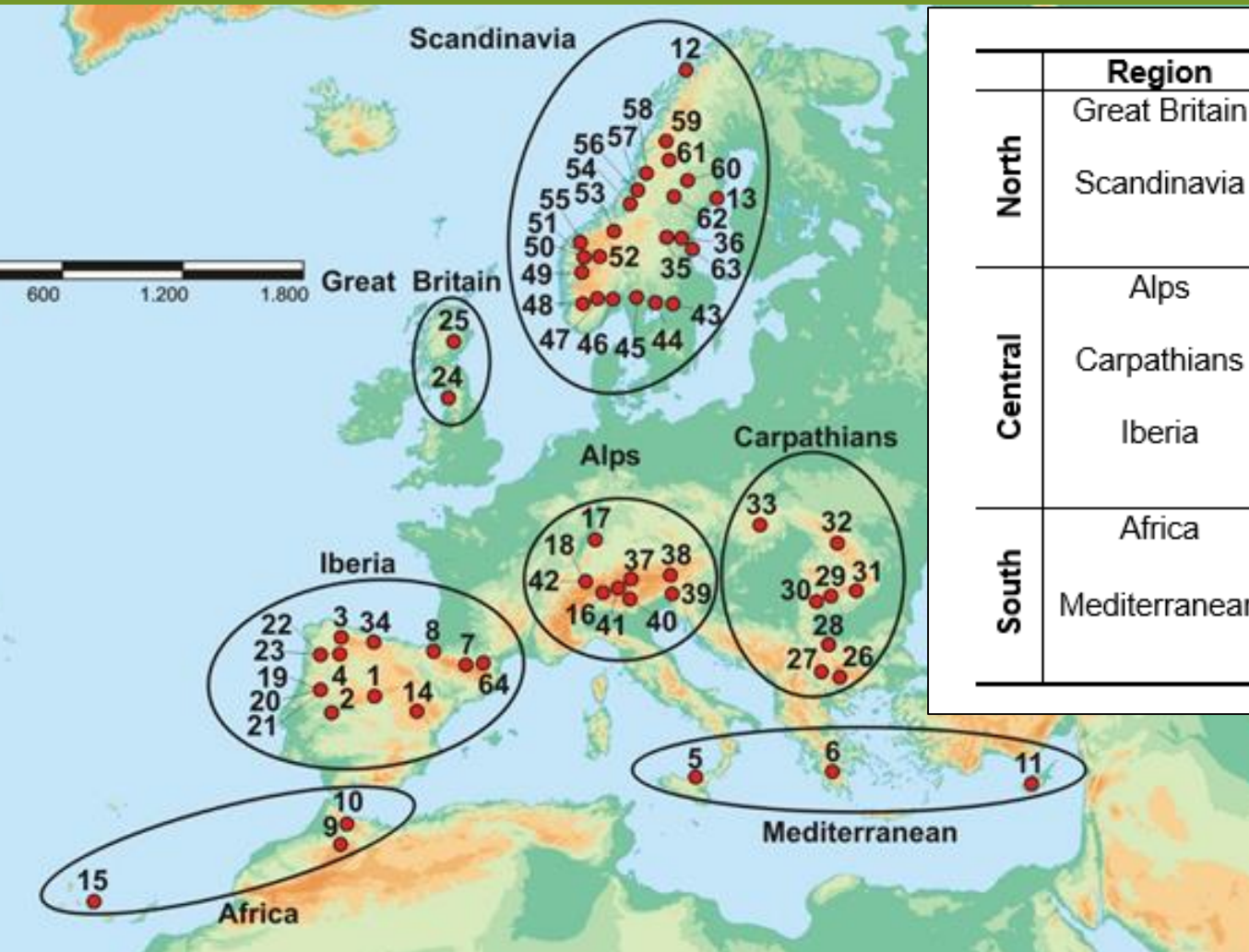
**Table S5.** Allelic richness (AR) and private allelic richness (PAR) detected in each type of substrate. Standard deviations are showed in brackets.

	Twigs		Branches		Trunks		Rock				
	AR	PAR	AR	PAR	AR	PAR	AR	PAR			
n:203	5.93	0.57	n: 30	3.57	0.07	n:256	6.07	0.68	n: 37	2.79	0.00
	(1.15)	(0.21)		(0.63)	(0.07)		(1.15)	(0.29)		(0.39)	(0.00)
AR/n	0.029	-	AR/n	0.119	-	AR/n	0.024	-	AR/n	0.075	-

## Allelic richness

Higher diversity within populations than among.  
Similar diversity in trunks and twigs.

# Population genetics in *Bryoria fuscescens*



	Region	specimens	AR	PAR	specimens	AR	PAR		
North	Great Britain	32	2.642	0.000	588	7.500	1.357		
	Scandinavia	556	(0.439)	(0.000)				(1.207)	(0.452)
Central	Alps	189	5.357	0.357	641	7.071	0.857		
	Carpathians	179	(1.014)	(0.199)				(1.442)	(0.274)
	Iberia	273	(0.976)	(0.000)				(0.125)	
South	Africa	65	4.571	0.428	130	5.571	0.500		
	Mediterranean	65	(0.947)	(0.227)				(1.087)	(0.251)

Scandinavia: ↑↑↑

Alps: ↑

Iberia: ↑

Carpathians: ↑↓

Great Britain: ↓

↑ High diversity

↓ Low diversity



# Population genetics in *Bryoria fuscescens*

- Less clonality than expected
- Saxicolous populations are genetically poor.
- Apotheciated populations are not significantly more diverse.
- Human activities can increase genetic diversity.
- Recent colonization signals
- Putative sexual reproduction in non apotheciated populations.

**Table 2.** Results of the analyses for each population, indicating the number of specimens (n), number of non-clonal specimens, percentage of polymorphic loci, unbiased haploid genetic diversity (uh), unbiased measure of linkage disequilibrium (rBarD, in bold = significant values with a p-value of 0.001), rarefied allelic richness (AR), rarefied private allelic richness (PAR), number of loci with negative values in the K-test (in bold = significant values with a p-value of 0.05), and putative population disturbances (-: well-preserved more or less uniform forest).

Population number	n	Non-clonal specimens	Polymorphic loci (%)	uh mean (stand. error)	rBarD	AR	PAR	K-test	Putative population disturbances
Pops. 1-13 not showed									
14	19	16	100 %	0.525 (0.038)	<b>0.224</b>	3.214 (0.350)	0.003 (0.003)	7	-
15	22	16	100 %	0.559 (0.053)	<b>0.128</b>	3.428 (0.571)	0.129 (0.088)	8	-
16	20	20	100 %	0.573 (0.033)	<b>0.126</b>	3.285 (0.333)	0.071 (0.071)	4	Some tourism, apothecia present
17	14	6	71 %	0.255 (0.066)	<b>0.221</b>	2.071 (0.245)	0.071 (0.071)	<b>14 expansion</b>	Apothecia present
18	23	16	100 %	0.519 (0.046)	<b>0.175</b>	3.285 (0.398)	0.000 (0.000)	5	Apothecia present
19	23	13	100 %	0.366 (0.053)	0.031	2.642 (0.289)	0.000 (0.000)	10	-
20	9	1	0 %	0.000 (0.000)	NA	1.000 (0.000)	0.000 (0.000)	<b>14 expansion</b>	Saxicolous
21	10	1	0 %	0.000 (0.000)	NA	1.000 (0.000)	0.000 (0.000)	<b>14 expansion</b>	Saxicolous
22	23	4	71 %	0.276 (0.059)	<b>0.380</b>	1.928 (0.188)	0.000 (0.000)	<b>11 expansion</b>	Village close, apothecia present
23	23	5	86 %	0.356 (0.057)	<b>0.183</b>	2.000 (0.148)	0.000 (0.000)	7	Near pastures
24	9	5	64 %	0.317 (0.079)	<b>0.258</b>	2.071 (0.286)	0.000 (0.000)	10	Artificial forest
25	23	14	71 %	0.375 (0.072)	<b>0.096</b>	2.214 (0.317)	0.002 (0.002)	7	-
26	23	21	100 %	0.505 (0.046)	<b>0.268</b>	3.357 (0.378)	0.000 (0.000)	7	Some tourism, apothecia present
27	23	21	93 %	0.451 (0.063)	0.023	3.071 (0.412)	0.000 (0.000)	8	Human activities and constructions
28	23	18	100 %	0.466 (0.041)	<b>0.336</b>	3.214 (0.350)	0.002 (0.002)	6	Tourism
29	23	23	100 %	0.494 (0.057)	<b>0.144</b>	3.571 (0.387)	0.008 (0.008)	10	Human constructions, apothecia present
30	22	20	86 %	0.337 (0.072)	0.034	2.857 (0.333)	0.008 (0.008)	<b>12 expansion</b>	Apothecia present
31	23	20	100 %	0.056 (0.048)	<b>0.184</b>	3.785 (0.612)	0.000 (0.000)	5	Apothecia present
32	21	19	93 %	0.380 (0.068)	0.044	2.642 (0.371)	0.000 (0.000)	7	Apothecia present
Pops. 33-64 not showed									

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Population number	n	PAR	K-test	Putative population disturbances
Pops. 1-32				
14	13	0.003	7	-
15	9	0.088	8	-
16	11	0.071	4	Some tourism, apothecia present
17	11	0.071	<b>14 expansion</b>	Apothecia present
18	10	0.000	5	Apothecia present
19	10	0.000	10	-
20	10	0.000	<b>14 expansion</b>	Saxicolous
21	10	0.000	<b>14 expansion</b>	Saxicolous
22	10	0.000	<b>11 expansion</b>	Village close, apothecia present
23	10	0.000	7	Near pastures
24	10	0.000	10	Artificial forest
25	12	0.002	7	-
26	10	0.000	7	Some tourism, apothecia present
27	10	0.000	8	Human activities and constructions
28	12	0.002	6	Tourism
29	18	0.008	10	Human constructions, apothecia present
30	18	0.008	<b>12 expansion</b>	Apothecia present
31	10	0.000	5	Apothecia present
32	10	0.000	7	Apothecia present



Pops. 33-64 not showed  
 21 19 93% 0.380 0.044 2.642 0.000 (0.068) (0.457)

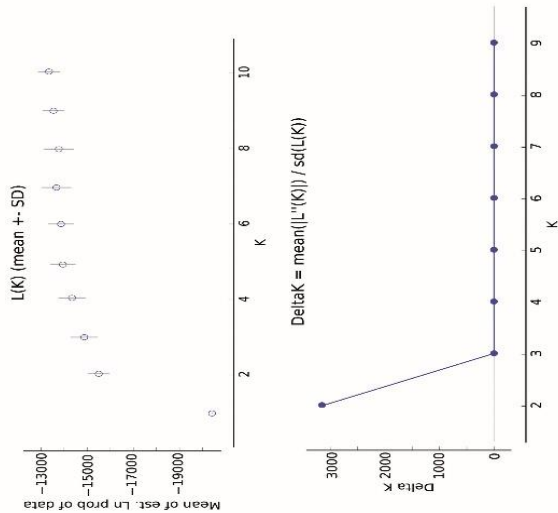
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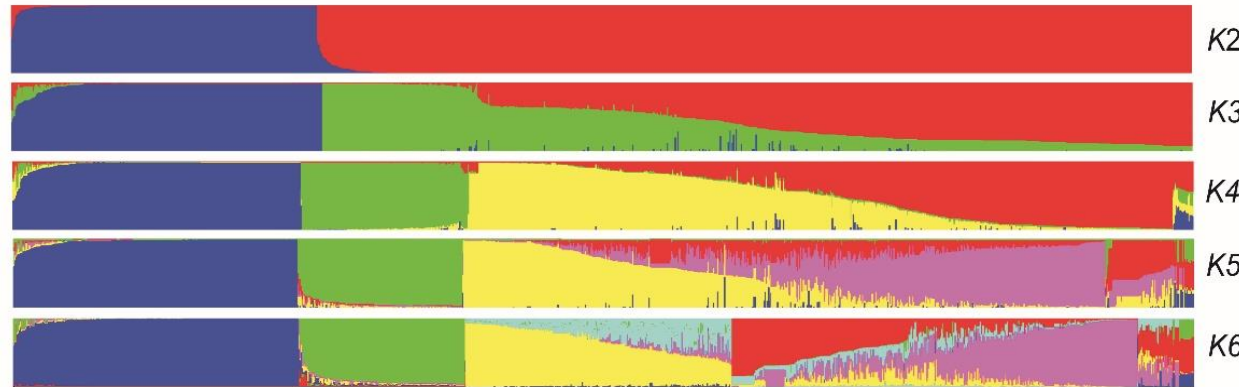
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17	14	6	71 %	0.255 (0.066)	<b>0.221</b>	2.071 (0.245)	0.071 (0.071)	<b>14 expansion</b>	Apothecia present
18	23	16	100 %	0.519 (0.046)	<b>0.175</b>	3.285 (0.398)	0.000 (0.000)	5	Apothecia present
19	23	13	100 %	0.366 (0.053)	0.031	2.642 (0.289)	0.000 (0.000)	10	-
20	9	1	0 %	0.000 (0.000)	NA	1.000 (0.000)	0.000 (0.000)	<b>14 expansion</b>	Saxicolous
21	10	1	0 %	0.000 (0.000)	NA	1.000 (0.000)	0.000 (0.000)	<b>14 expansion</b>	Saxicolous
22	23	4	71 %	0.276 (0.059)	<b>0.380</b>	1.928 (0.188)	0.000 (0.000)	<b>11 expansion</b>	Village close, apothecia present
23	23	5	86 %	0.356 (0.057)	<b>0.183</b>	2.000 (0.148)	0.000 (0.000)	7	Near pastures
24	9	5	64 %	0.317 (0.079)	<b>0.258</b>	2.071 (0.286)	0.000 (0.000)	10	Artificial forest
25	23	14	71 %	0.375 (0.072)	<b>0.096</b>	2.214 (0.317)	0.002 (0.002)	7	-
26	23	21	100 %	0.505 (0.046)	<b>0.268</b>	3.357 (0.378)	0.000 (0.000)	7	Some tourism, apothecia present
27	23	21	93 %	0.451 (0.063)	0.023	3.071 (0.412)	0.000 (0.000)	8	Human activities and constructions
28	23	18	100 %	0.466 (0.041)	<b>0.336</b>	3.214 (0.350)	0.002 (0.002)	6	Tourism
29	23	23	100 %	0.494 (0.057)	<b>0.144</b>	3.571 (0.387)	0.008 (0.008)	10	Human constructions, apothecia present
30	22	20	86 %	0.337 (0.072)	0.034	2.857 (0.333)	0.008 (0.008)	<b>12 expansion</b>	Apothecia present
31	23	20	100 %	0.056 (0.048)	<b>0.184</b>	3.785 (0.612)	0.000 (0.000)	5	Apothecia present
32	21	19	93 %	0.380 (0.068)	0.044	2.642 (0.371)	0.000 (0.000)	7	Apothecia present
Pops. 33-64 not showed									

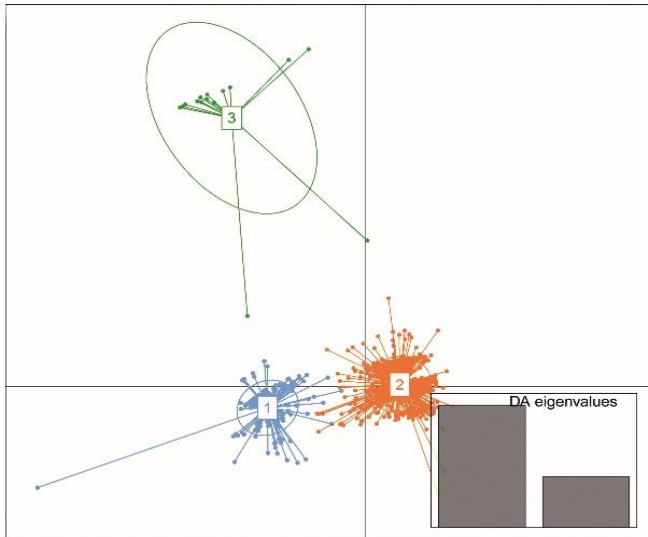
# Population genetics in *Bryoria fuscescens*



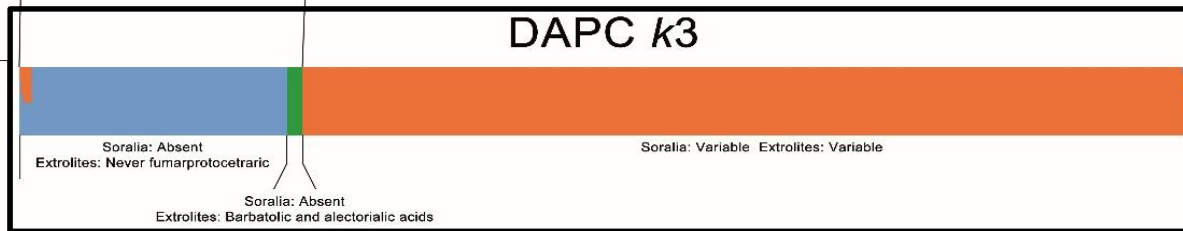
STRUCTURE  $k2-k6$



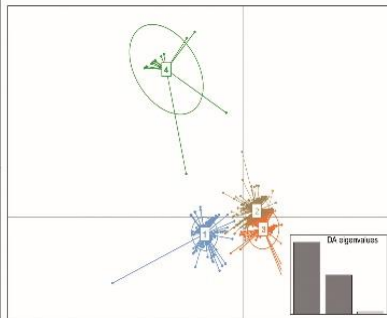
DAPC  $k3$



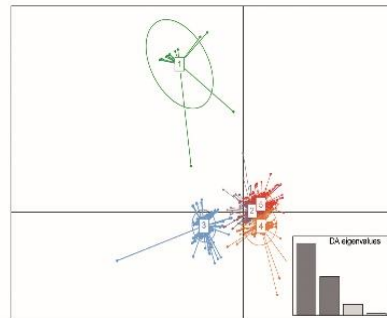
DAPC  $k3$



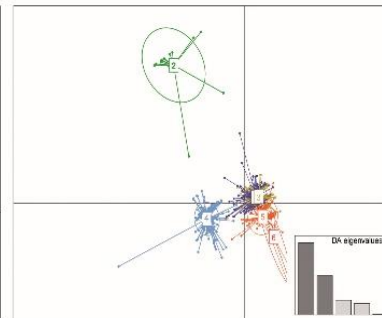
DAPC  $k4$



DAPC  $k5$



DAPC  $k6$



**Best gene pools:**  
**DAPC K3**

**Genepool 1**

Soralia: Frequent  
Fum.: Variable  
Ph. *capillaris*: 13%  
Ph. *fuscescens*: 87%

**Genepool 2**

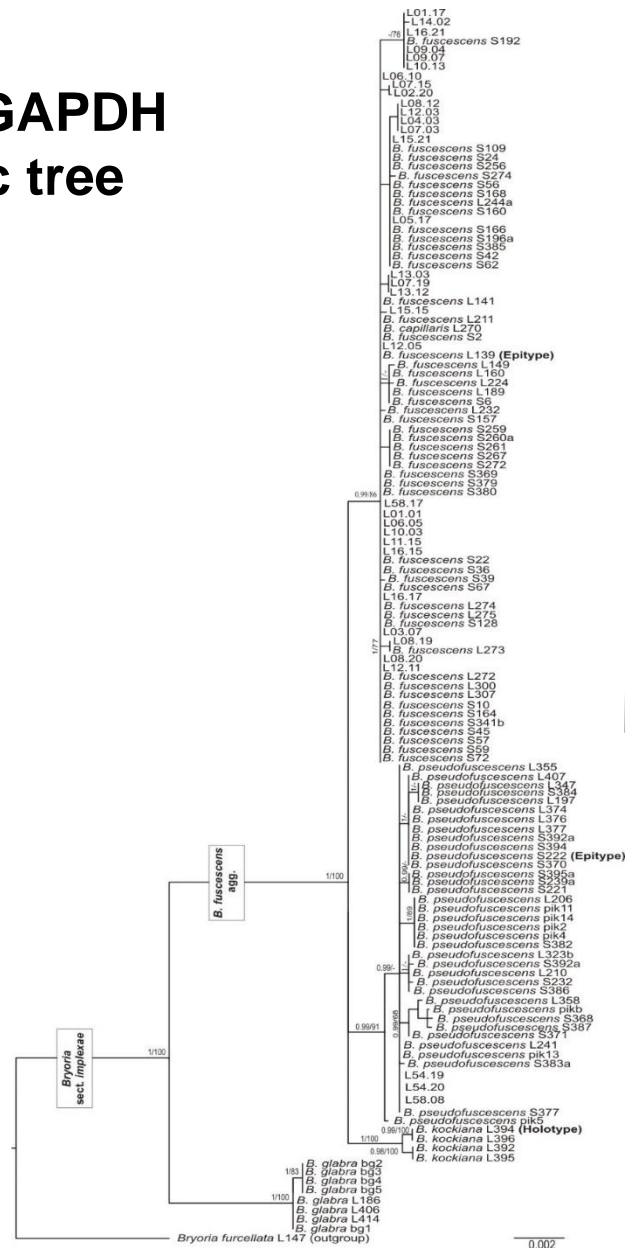
Soralia: Absent  
Fum.: No  
Ph. *capillaris*: 87%  
Ph. *fuscescens*: 13%

**Genepool 3**

Soralia: Absent  
Fum.: No  
Ph. *capillaris*: 100%  
Ph. *fuscescens*: 0%

# Population genetics in *Bryoria fuscescens*

nuITS, IGS & GAPDH  
Phylogenetic tree



*Bryoria fuscescens*

*B. pseudofuscescens*

*B. kockiana*

**Best gene pools:**

**DAPC K3**

**Genepool 1**

Soralia: Frequent

Fum.: Variable

Ph. *capillaris*: 13%

Ph. *fuscescens*: 87%

**Genepool 2**

Soralia: Absent

Fum.: No

Ph. *capillaris*: 87%

Ph. *fuscescens*: 13%

**Genepool 3**

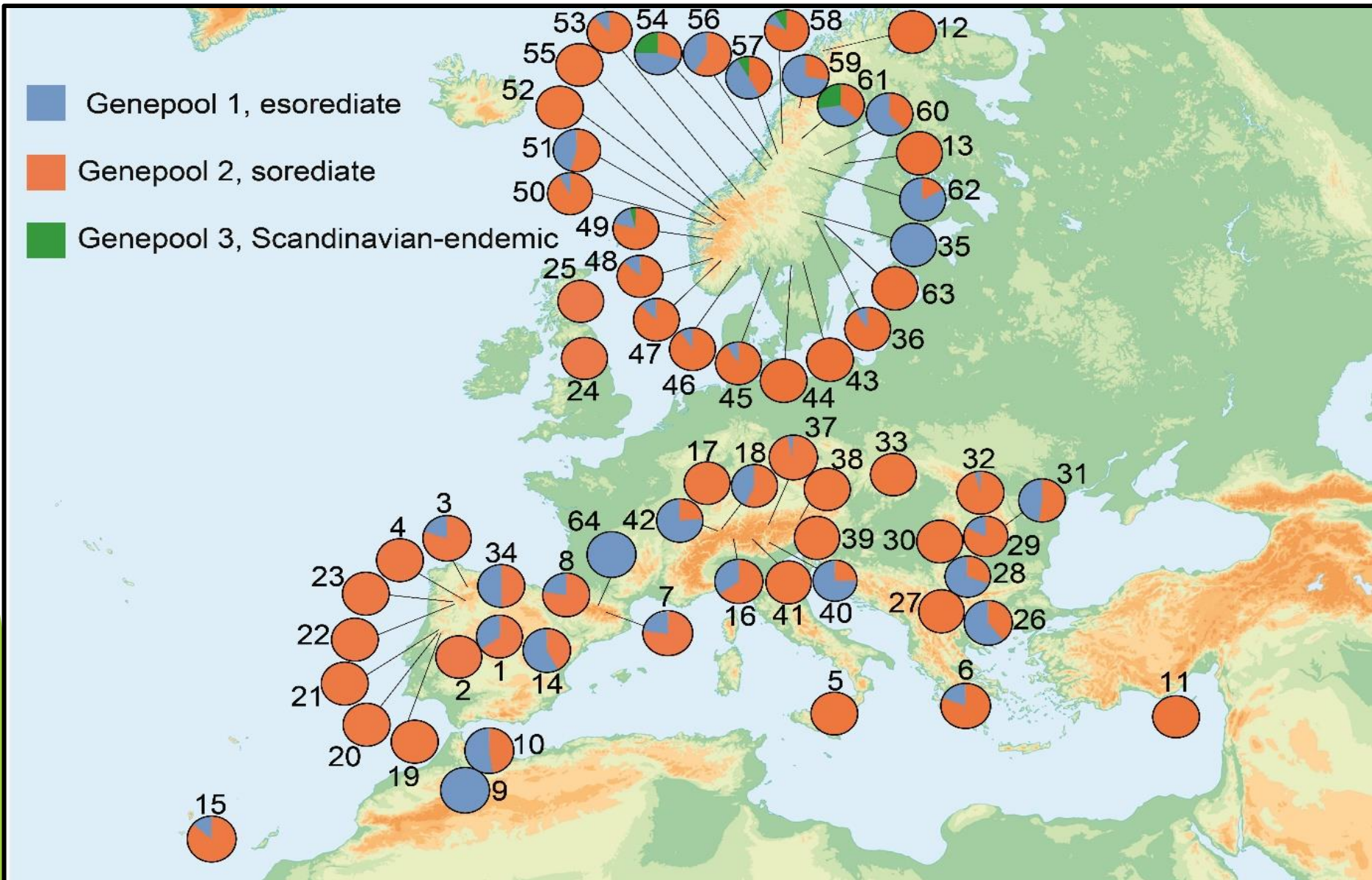
Soralia: Absent

Fum.: No

Ph. *capillaris*: 100%

Ph. *fuscescens*: 0%

# Population genetics in *Bryoria fuscescens*



## Best genepools:

### DAPC K3

#### Genepool 1

Soralia: Frequent

Fum.: Variable

Ph. *capillaris*: 13%

Ph. *fuscescens*: 87%

#### Genepool 2

Soralia: Absent

Fum.: No

Ph. *capillaris* : 87%

Ph. *fuscescens* : 13%

#### Genepool 3

Soralia: Absent

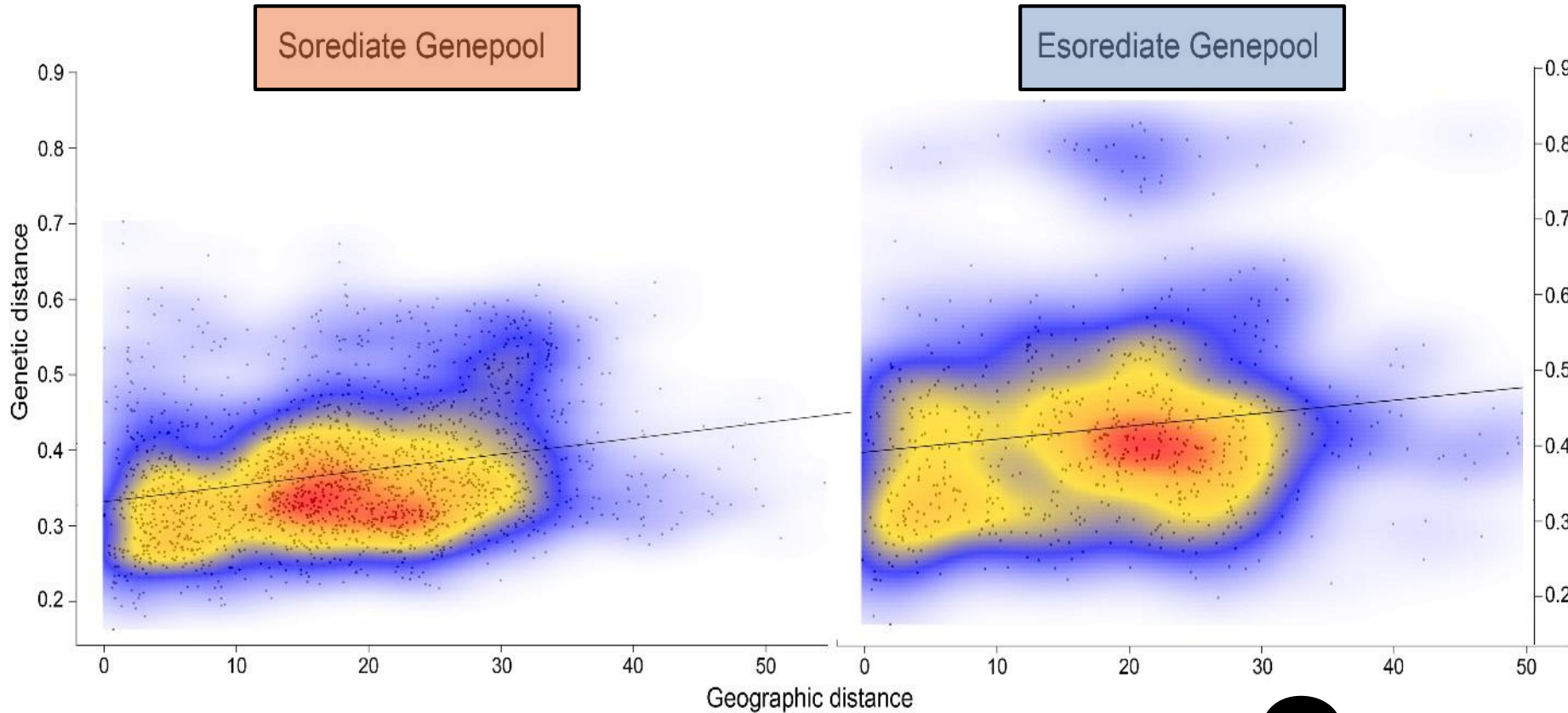
Fum.: No

Ph. *capillaris* : 100%

Ph. *fuscescens* : 0%

# Population genetics in *Bryoria fuscescens*

Analysis to detect genetic isolation by geographic distance between pairs of populations



Soralia are not favouring dispersion



**Best genepools:**  
**DAPC K3**

**Genepool 1**

**Soralia: Frequent**  
**Fum.: Variable**  
**Ph. *capillaris*: 13%**  
**Ph. *fuscescens*: 87%**

**Genepool 2**

**Soralia: Absent**  
**Fum.: No**  
**Ph. *capillaris* : 87%**  
**Ph. *fuscescens* : 13%**

**Genepool 3**

**Soralia: Absent**  
**Fum.: No**  
**Ph. *capillaris* : 100%**  
**Ph. *fuscescens* : 0%**

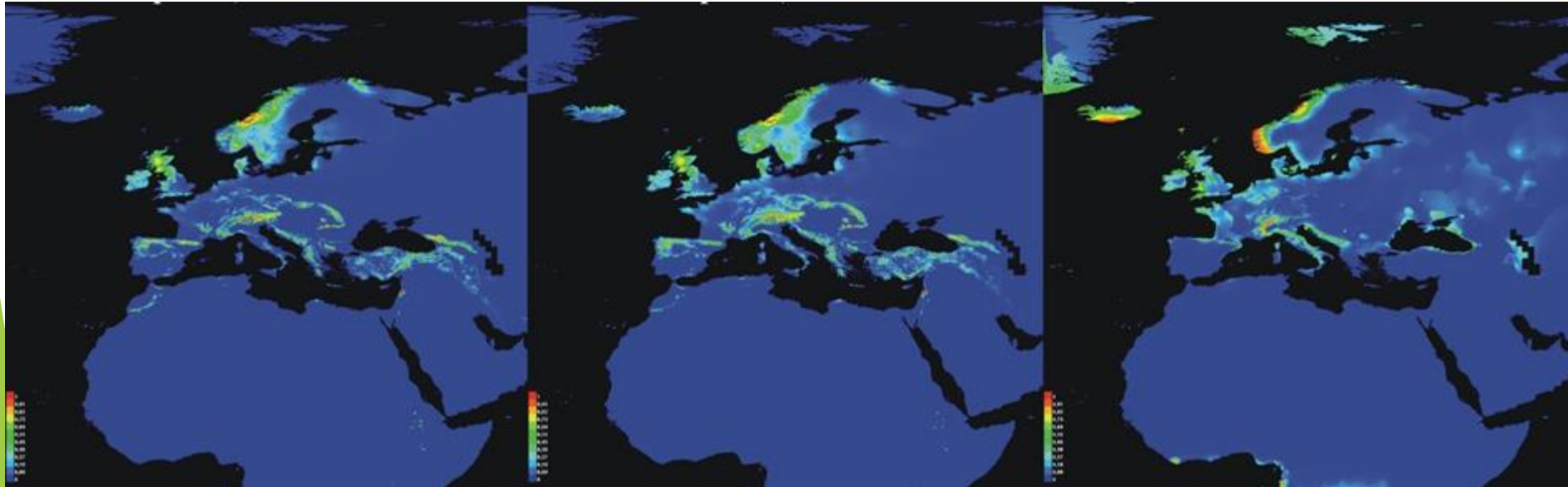
# Population genetics in *Bryoria fuscescens*

Potential distribution prediction for each Genepool using Maxent and 11 bioclimatic layers

Genepool 1

Genepool 2

Genepool 3



Phenotype-*fuscescens*

Phenotype-*capillaris*

*B. fuscescens*-*pseudofuscescens*

**Best genepools:**  
**DAPC K3**

**Genepool 1**

Soralia: Frequent

Fum.: Variable

Ph. *capillaris*: 13%

Ph. *fuscescens*: 87%

**Genepool 2**

Soralia: Absent

Fum.: No

Ph. *capillaris* : 87%

Ph. *fuscescens* : 13%

**Genepool 3**

Soralia: Absent

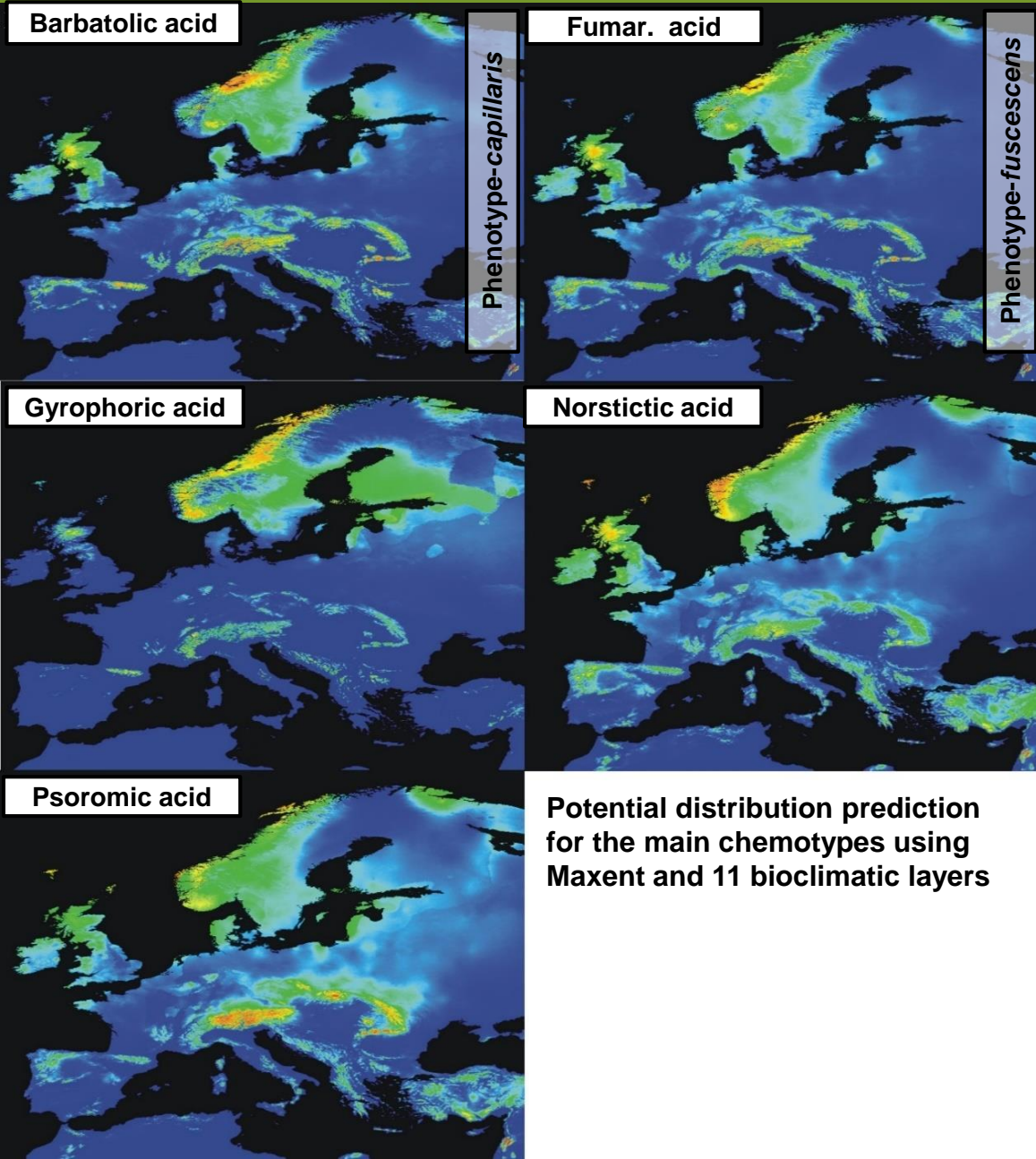
Fum.: No

Ph. *capillaris* : 100%

Ph. *fuscescens* : 0%



# Population genetics in *Bryoria fuscescens*



Potential distribution prediction for the main chemotypes using Maxent and 11 bioclimatic layers

## Genetically fixed

- Barbatolic acid
- Fumarprotocetraric acid

## Environmentally influenced

- Gyrophoric acid
- Norstictic acid
- Psoromic acid

## Best genepools: DAPC K3

### Genepool 1

Soralia: Frequent  
Fum.: Variable  
Ph. *capillaris*: 13%  
Ph. *fuscescens*: 87%

### Genepool 2

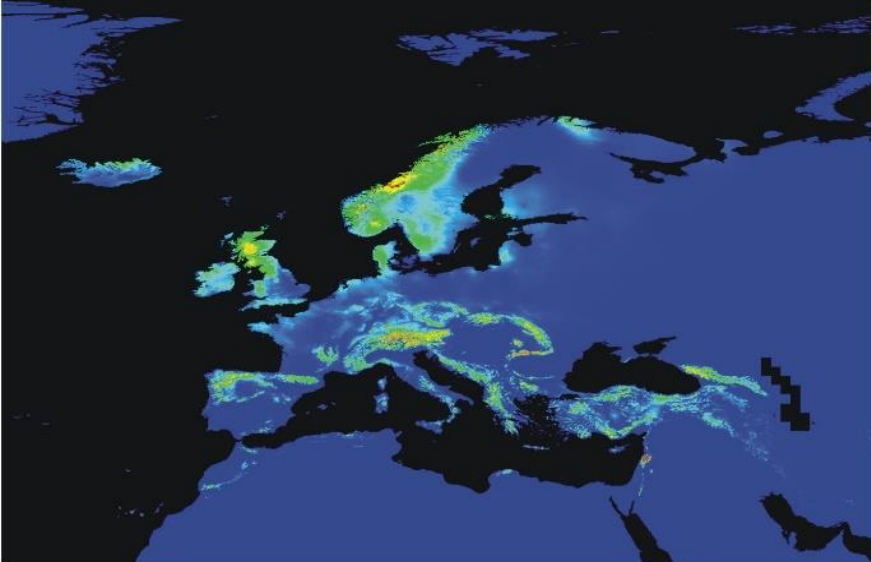
Soralia: Absent  
Fum.: No  
Ph. *capillaris* : 87%  
Ph. *fuscescens* : 13%

### Genepool 3

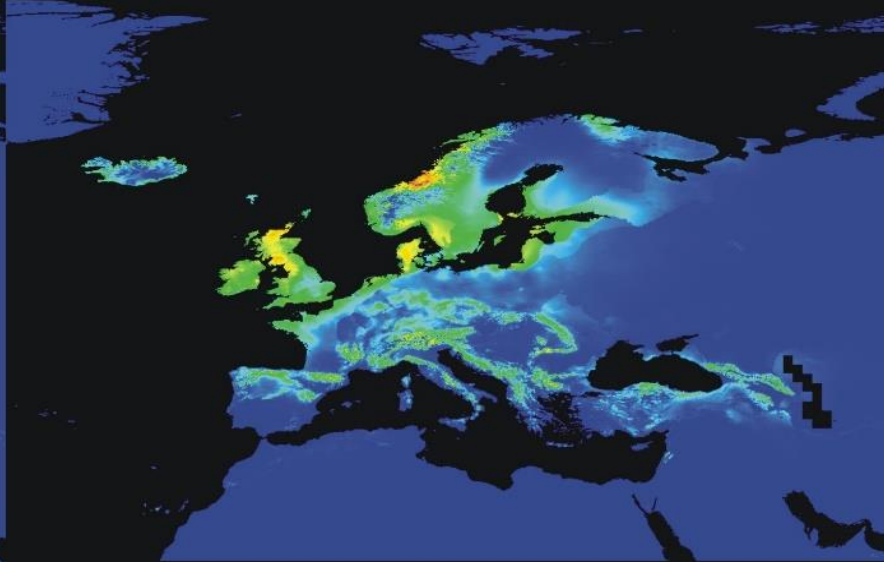
Soralia: Absent  
Fum.: No  
Ph. *capillaris* : 100%  
Ph. *fuscescens* : 0%

# Phylogeography of *Bryoria fuscescens*

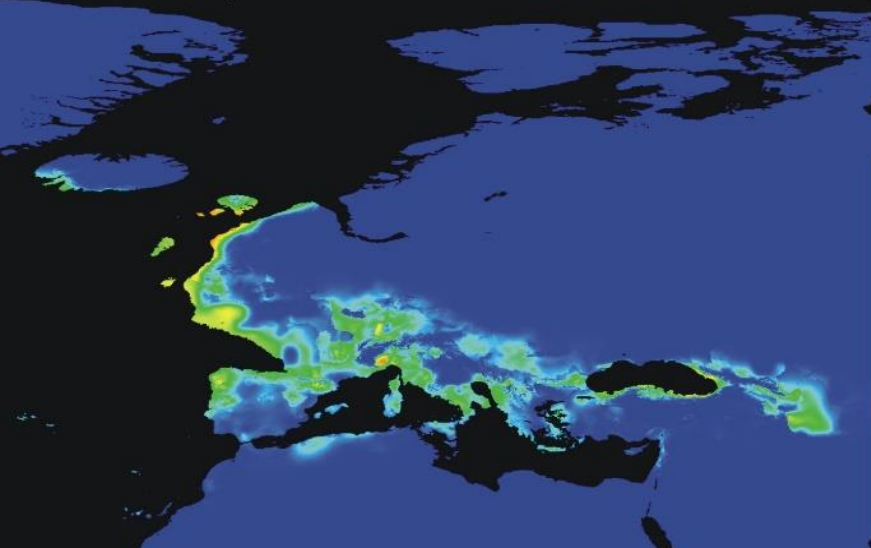
0 ya Current



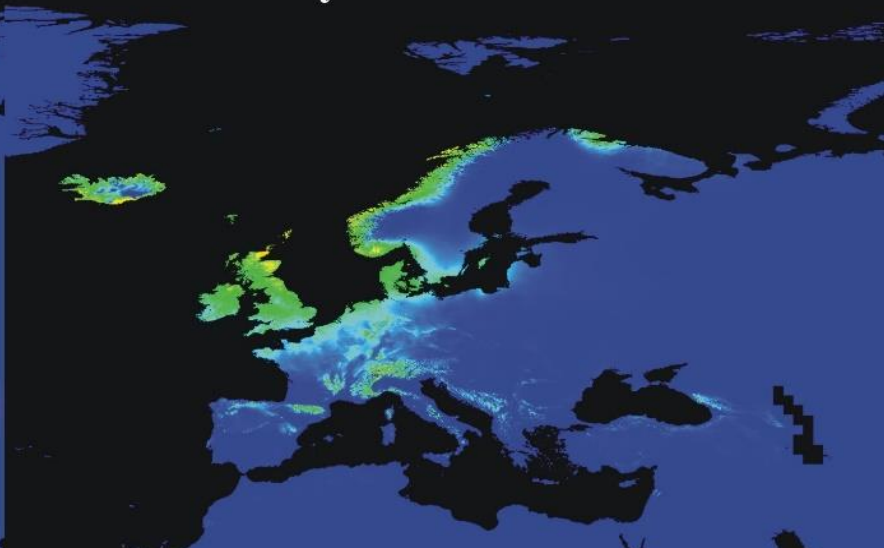
6 000 ya Mid-Holocene



22 000 ya Last Glacial Maximum



130 000 ya Last Inter-Glacial



Glacial refugia candidates:

East of British Isles

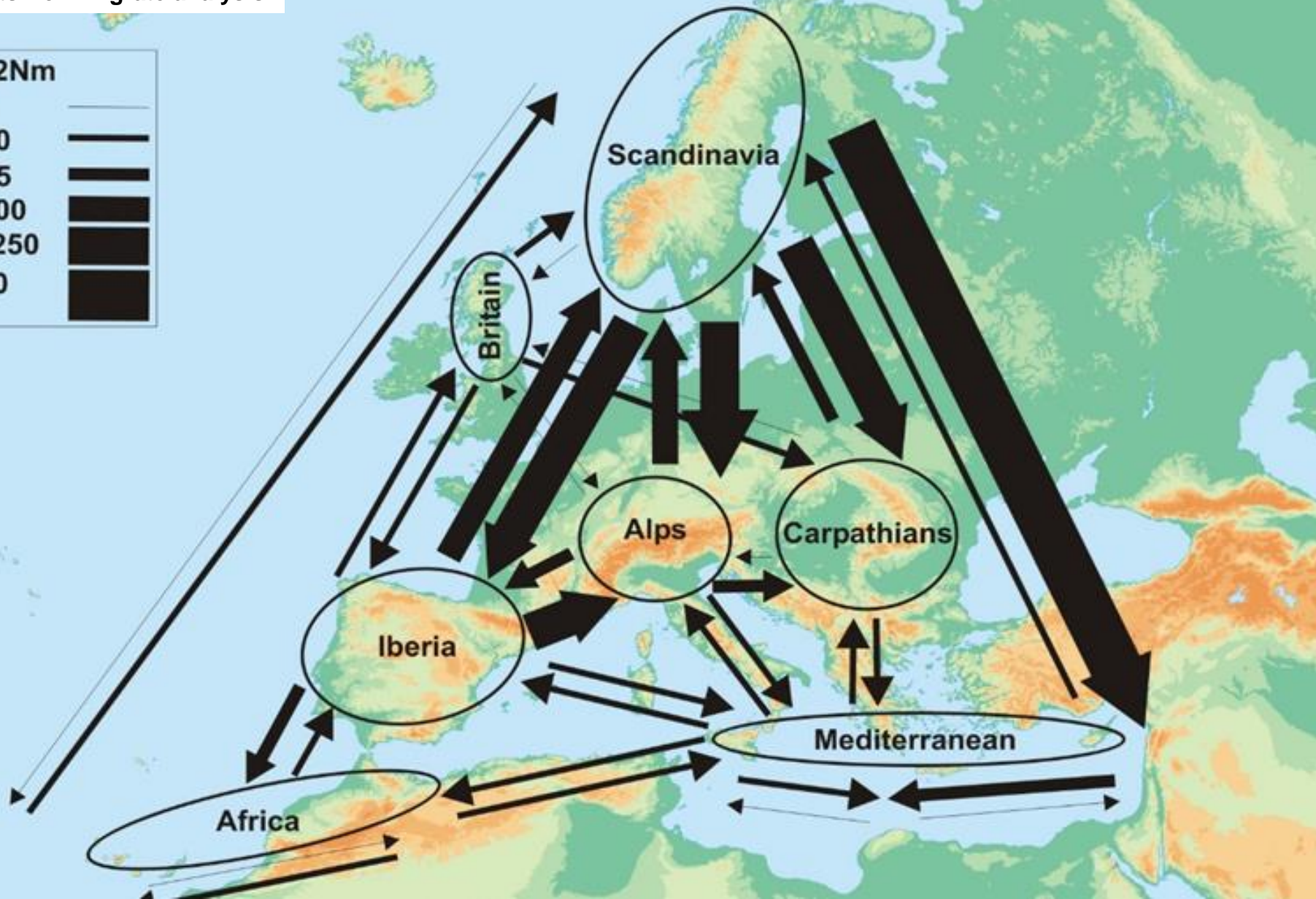
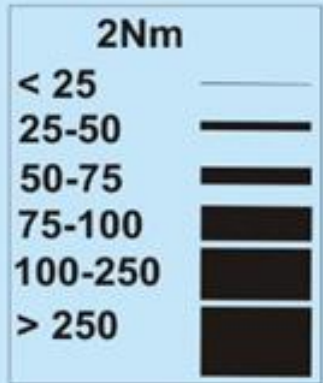
Northwest of Iberian Peninsula

Alps lowlands

Black sea

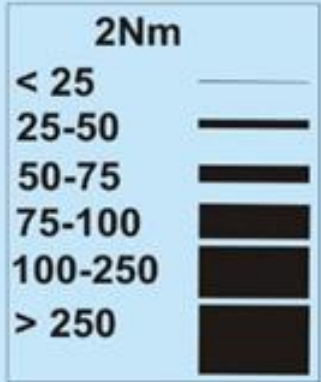
# Phylogeography of *Bryoria fuscescens*

Results from Migrate analysis

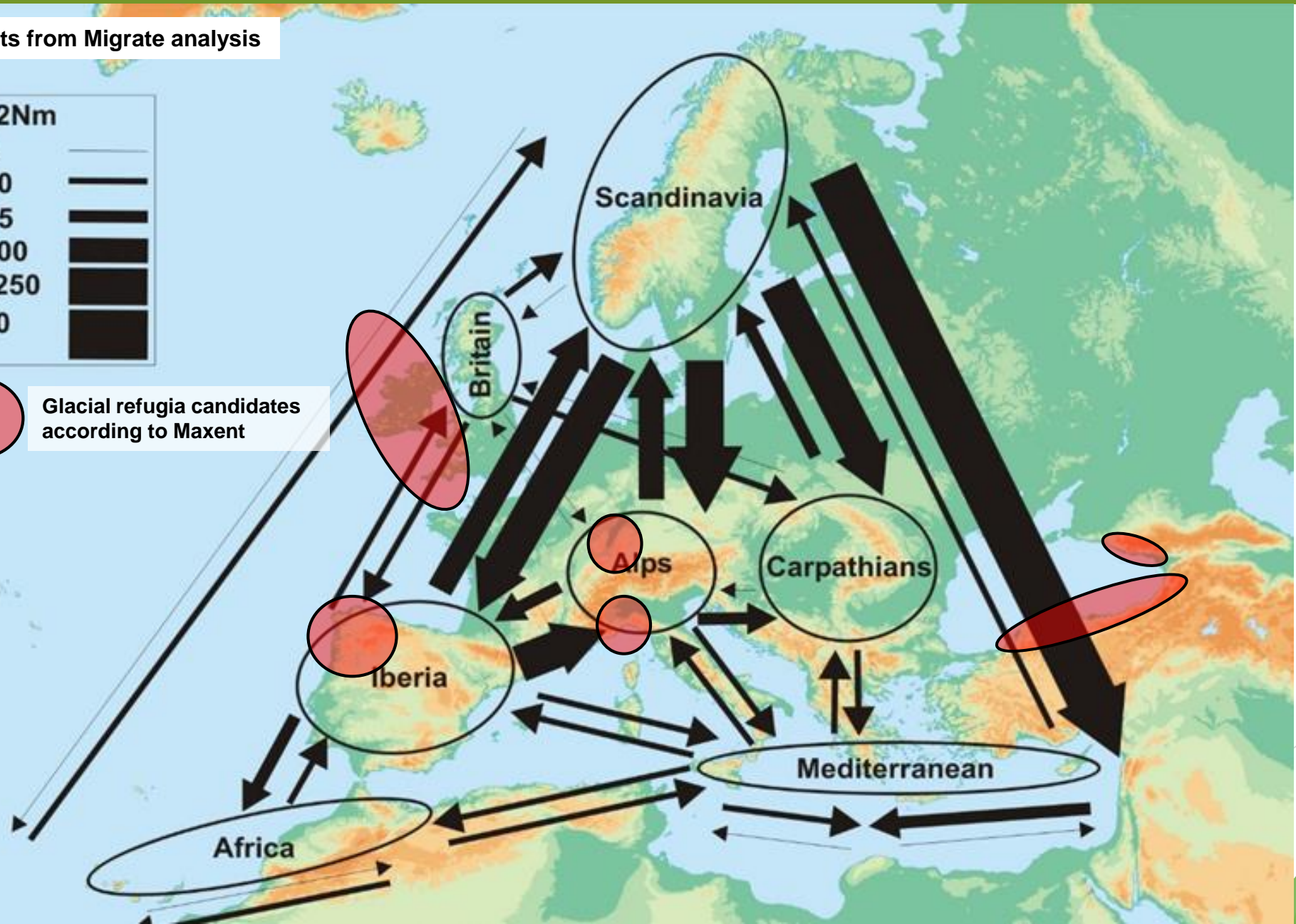


# Phylogeography of *Bryoria fuscescens*

Results from Migrate analysis

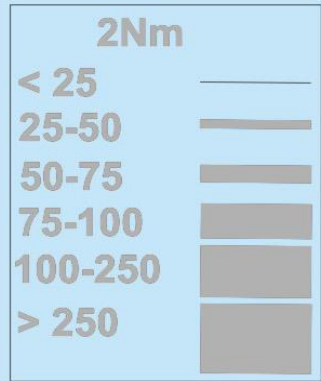


Glacial refugia candidates according to Maxent



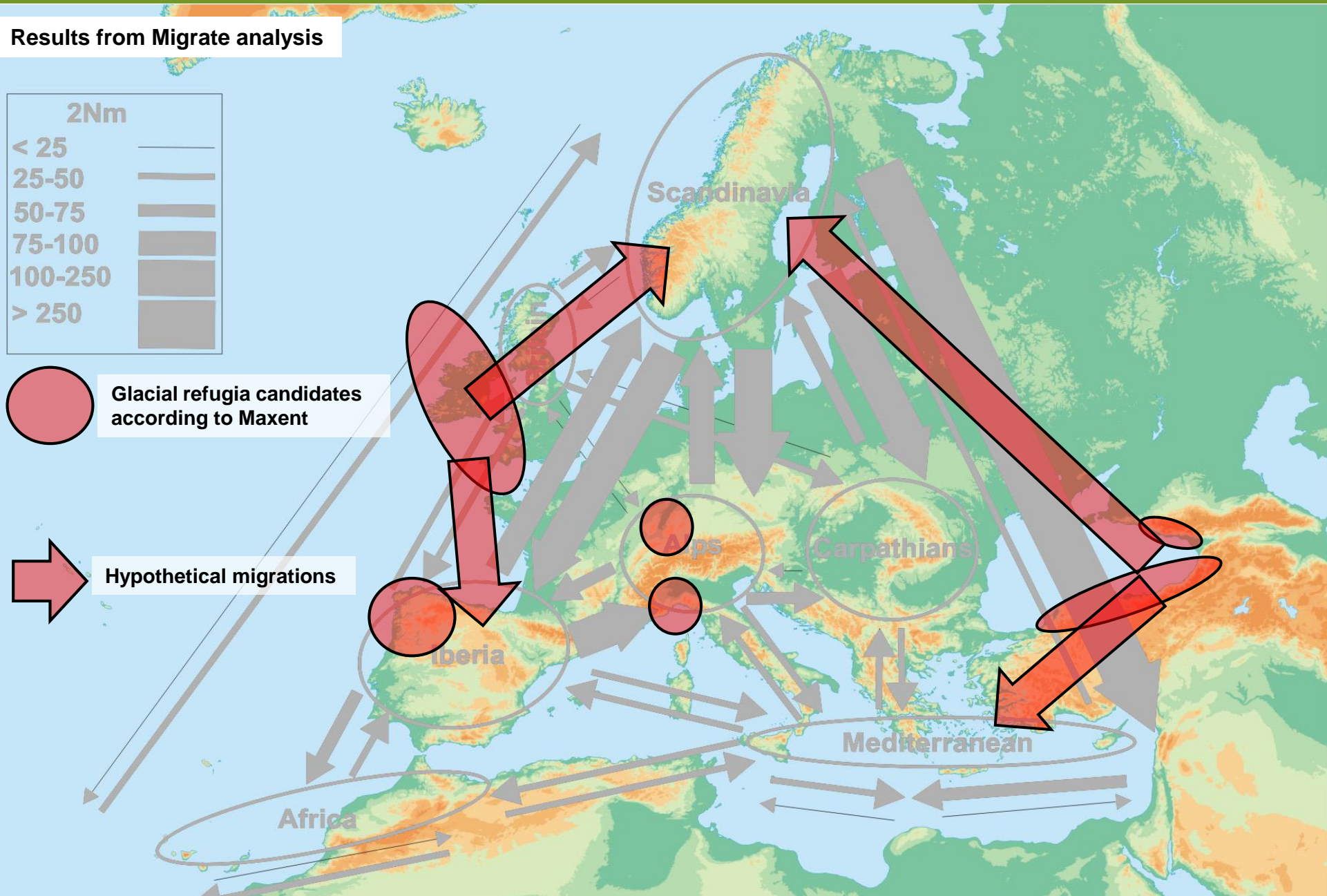
# Phylogeography of *Bryoria fuscescens*

Results from Migrate analysis



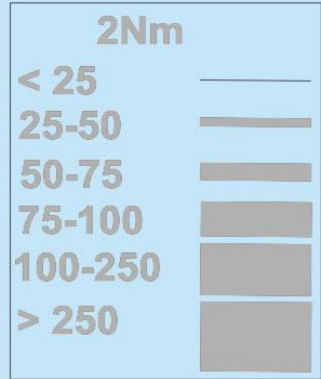
Glacial refugia candidates according to Maxent

Hypothetical migrations



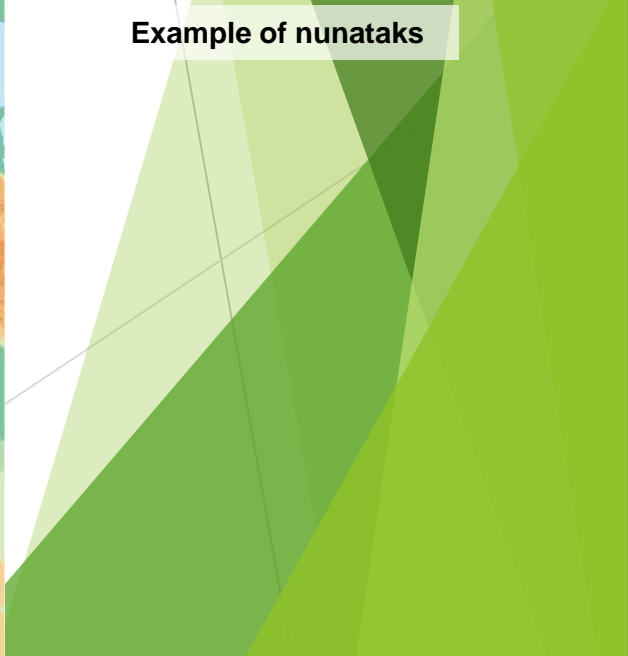
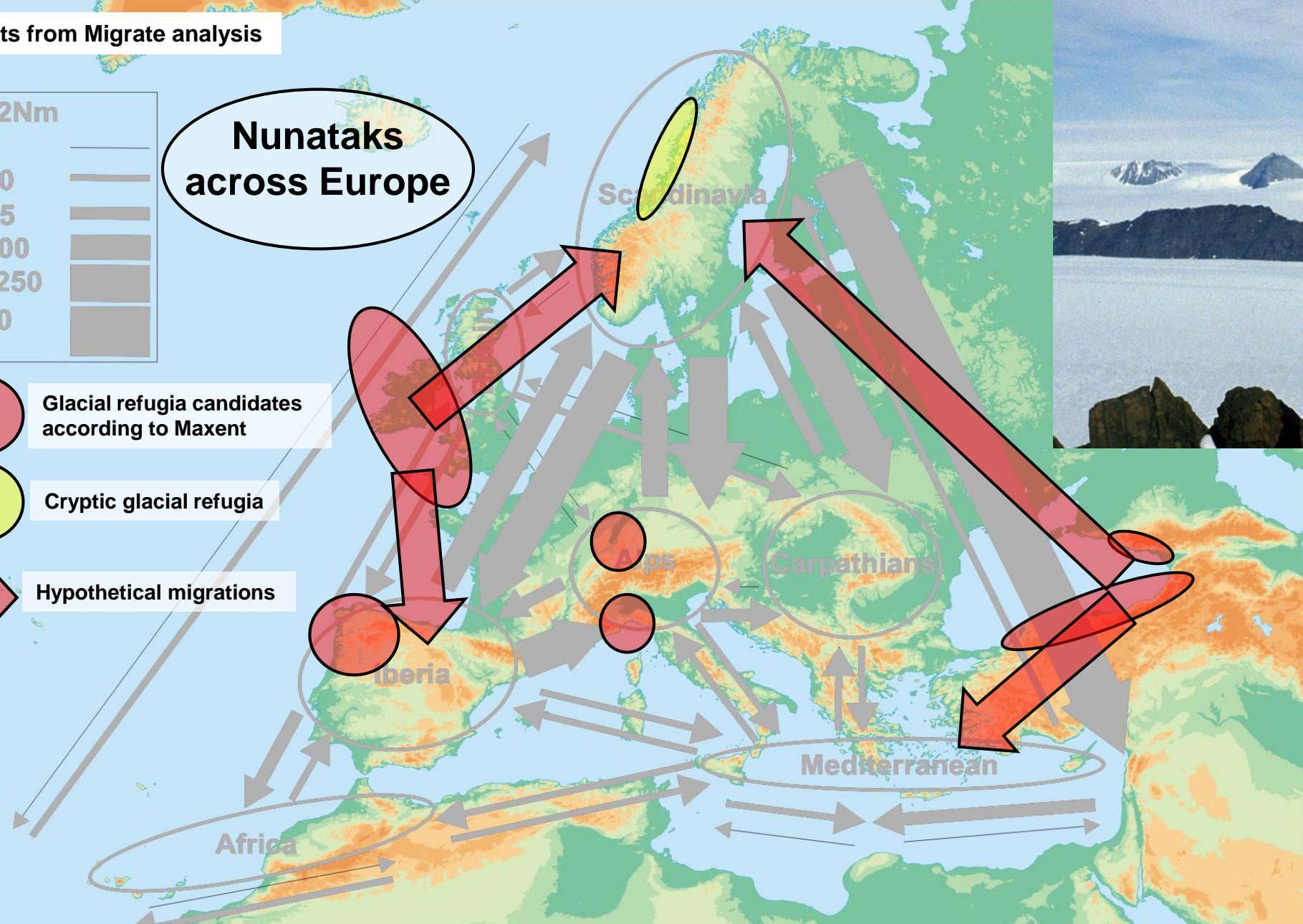
# Phylogeography of *Bryoria fuscescens*

Results from Migrate analysis



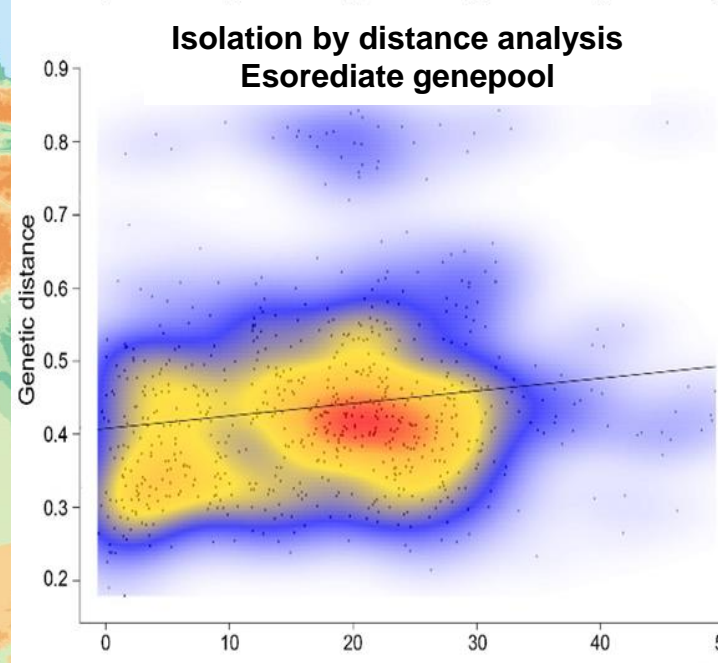
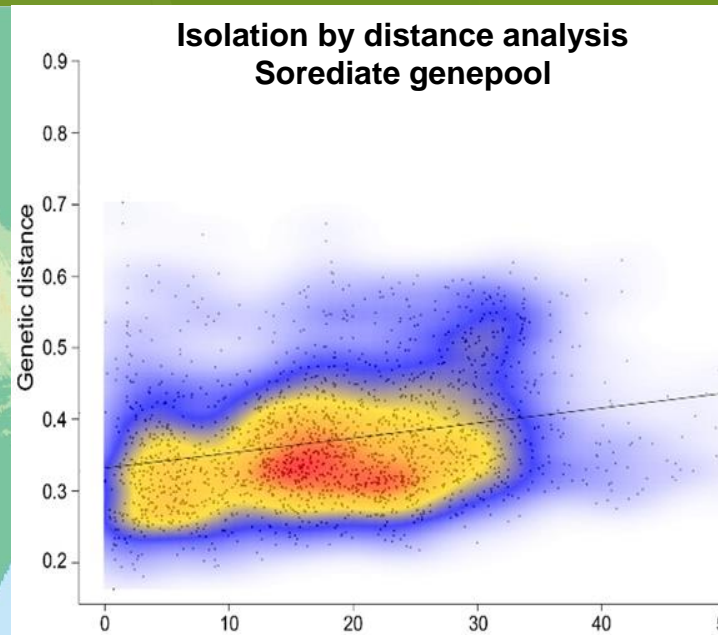
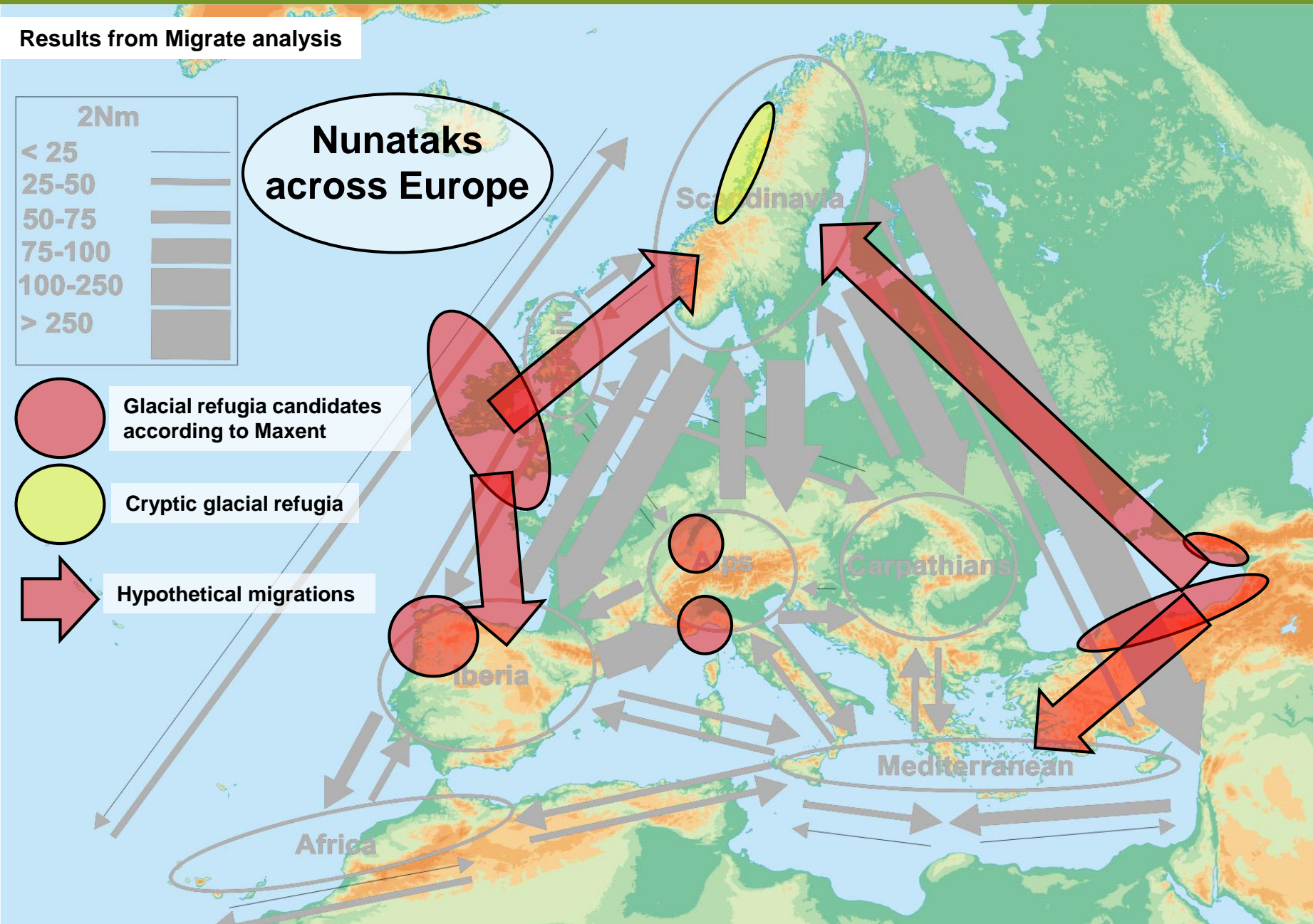
Nunataks  
across Europe

- Glacial refugia candidates according to Maxent
- Cryptic glacial refugia
- Hypothetical migrations



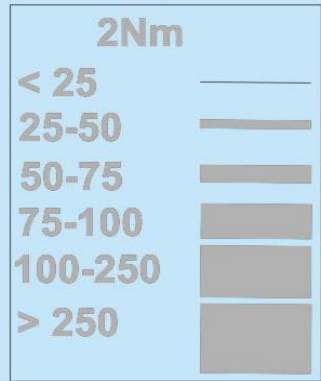
Example of nunataks

# Phylogeography of *Bryoria fuscescens*



# Phylogeography of *Bryoria fuscescens*

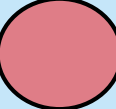


Results from Migrate analysis



Nunataks  
across Europe

Scandinavia

Africa

-  Glacial refugia candidates according to Maxent
-  Cryptic glacial refugia
-  Hypothetical migrations

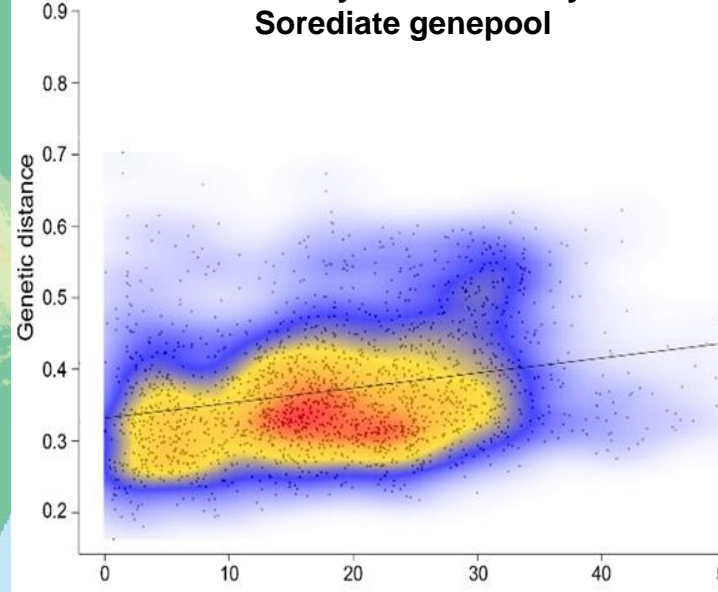
## Migration:

Far pair populations much more differentiated than closer ones.

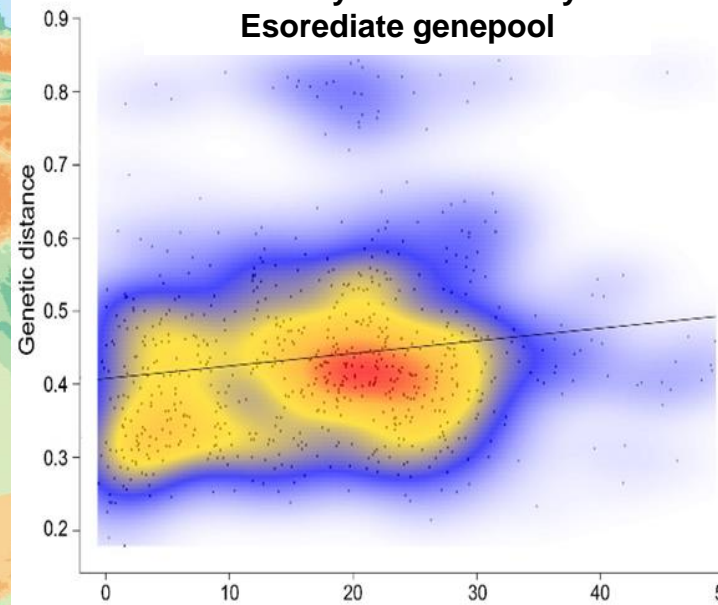
## Ancestral shared alleles:

Far pair populations not much more differentiated than closer ones.  
(usually linked to incomplete lineage sorting)

Isolation by distance analysis  
Sorediate genepool

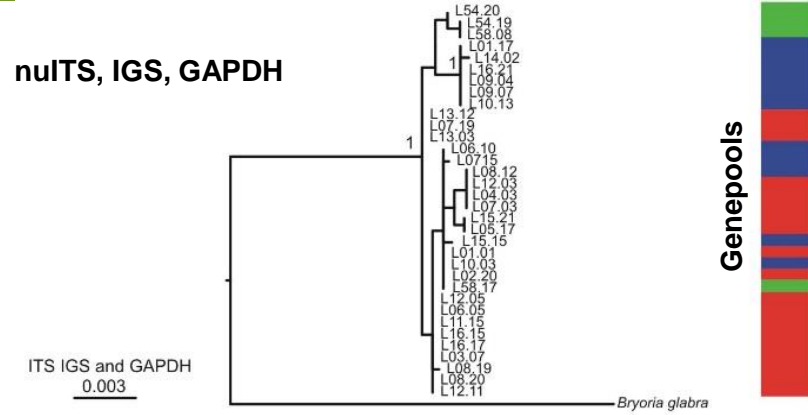


Isolation by distance analysis  
Esorediate genepool

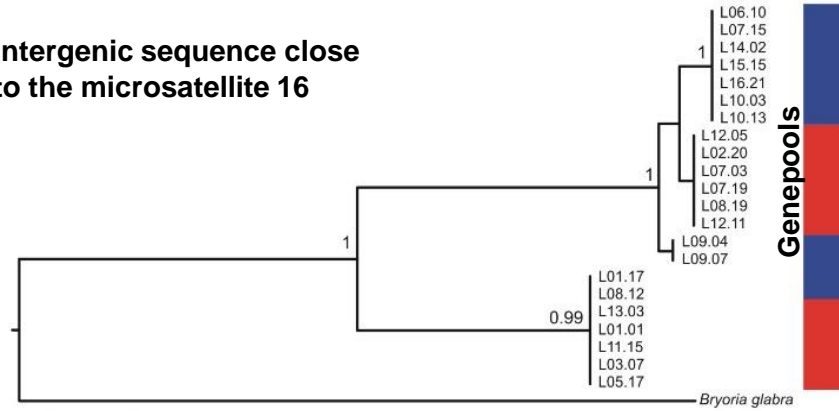




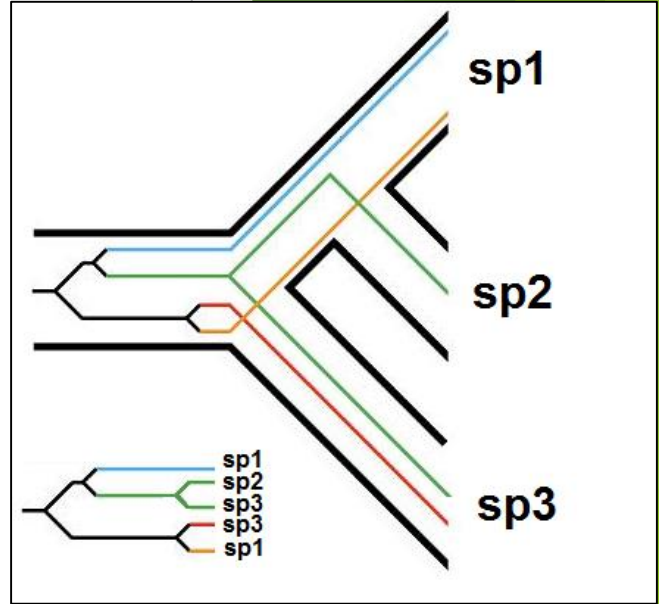
# Phylogeography of *Bryoria fuscescens*



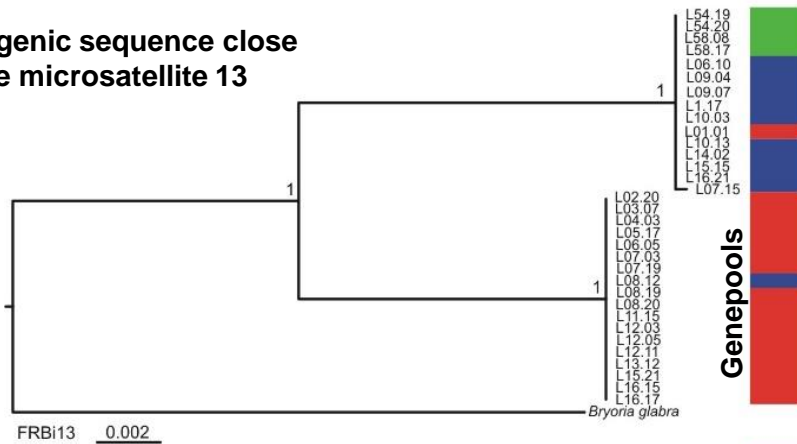
Intergenic sequence close to the microsatellite 16



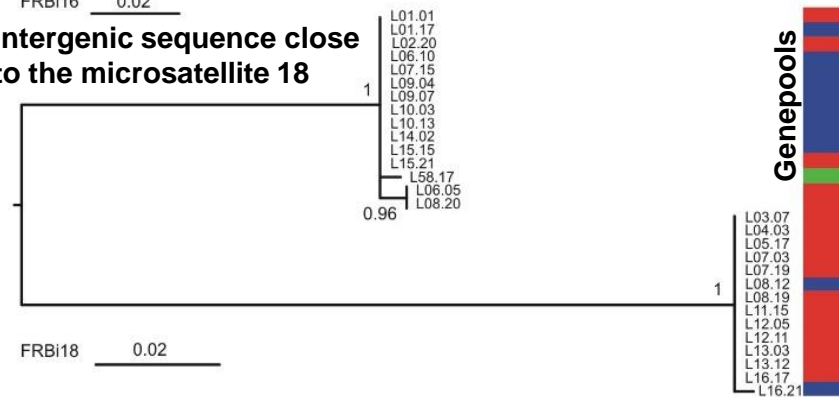
Evidence of incomplete lineage sorting



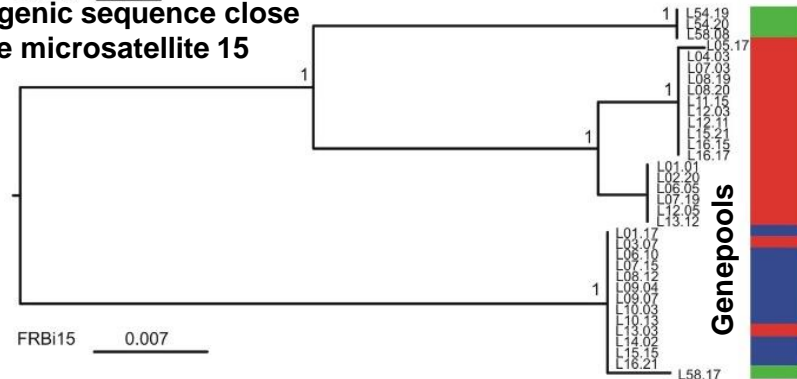
Intergenic sequence close to the microsatellite 13



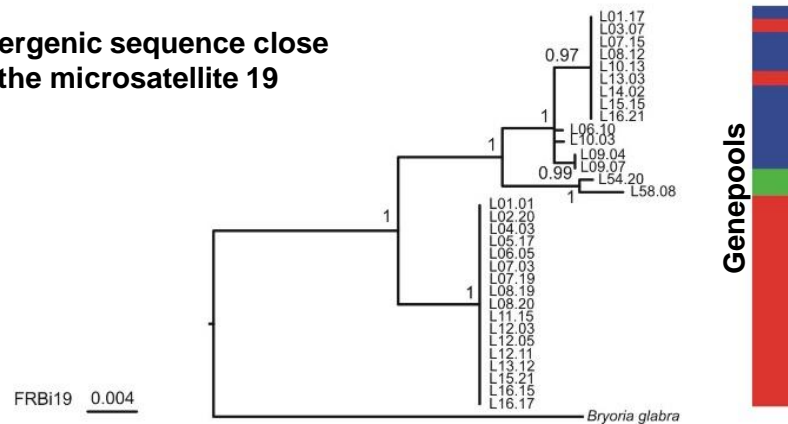
Intergenic sequence close to the microsatellite 18



Intergenic sequence close to the microsatellite 15

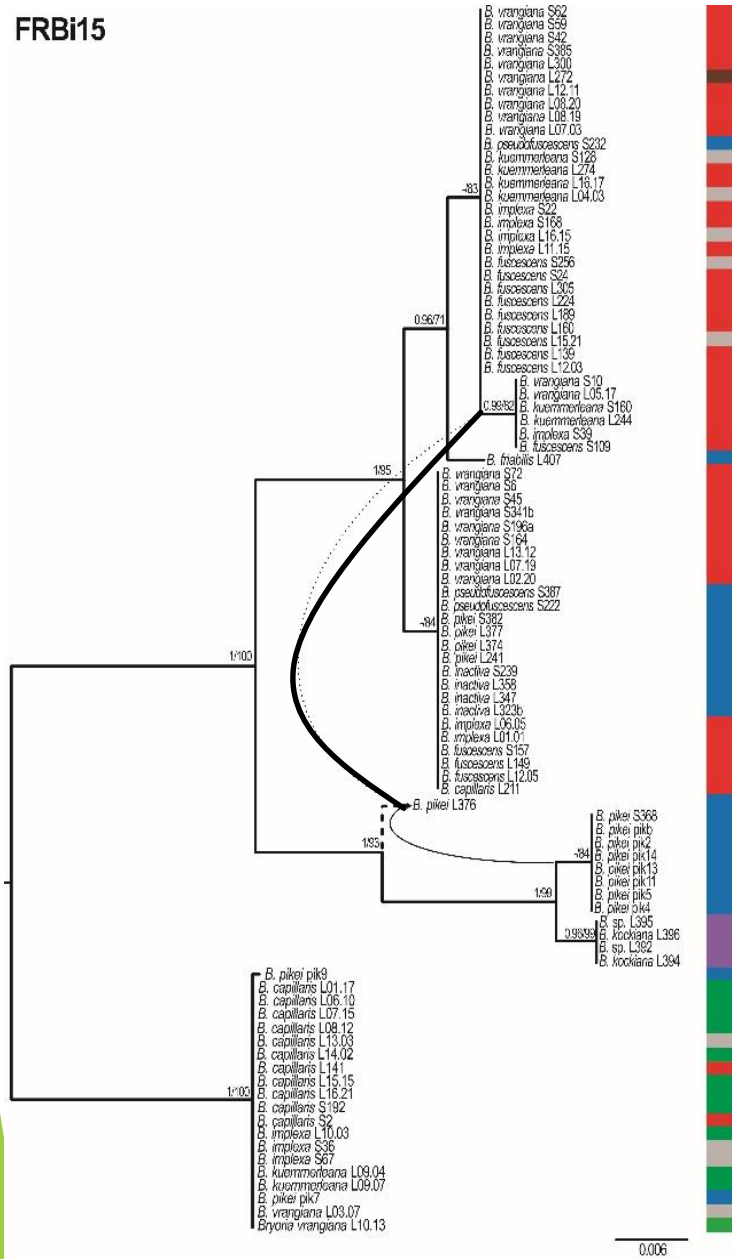


Intergenic sequence close to the microsatellite 19

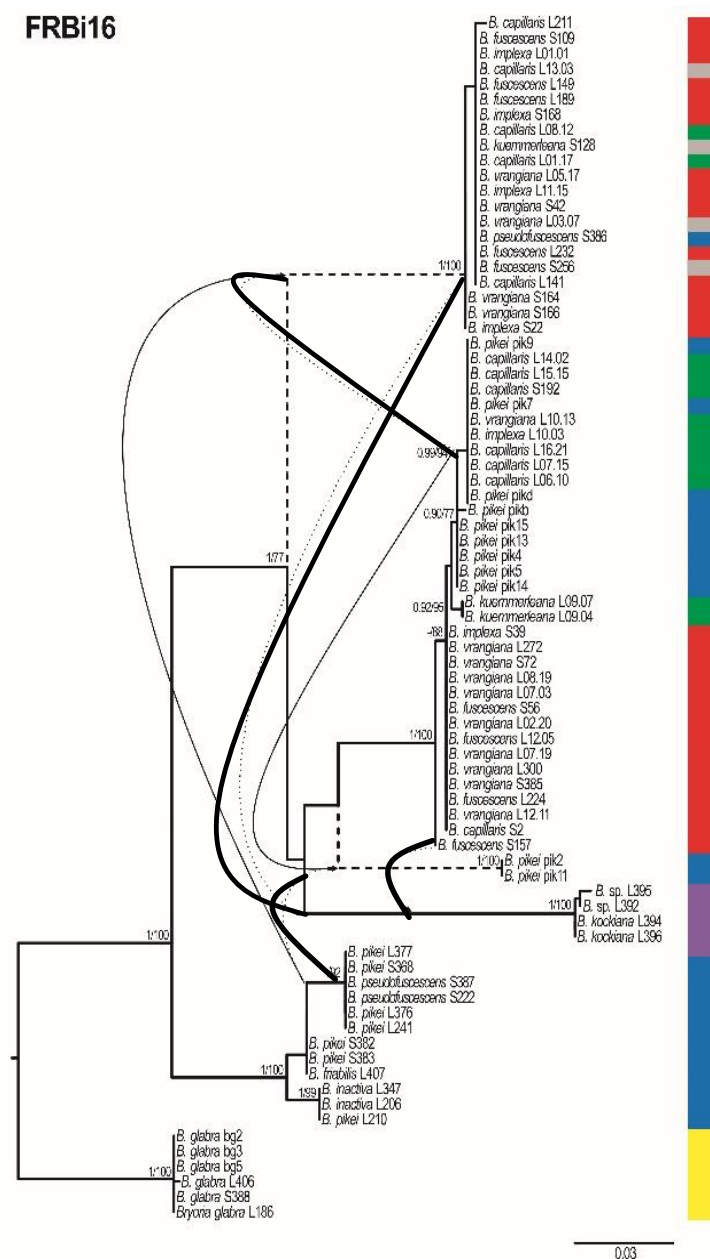


# Phylogeography of *Bryoria fuscescens*

FRBi15



FRBi16

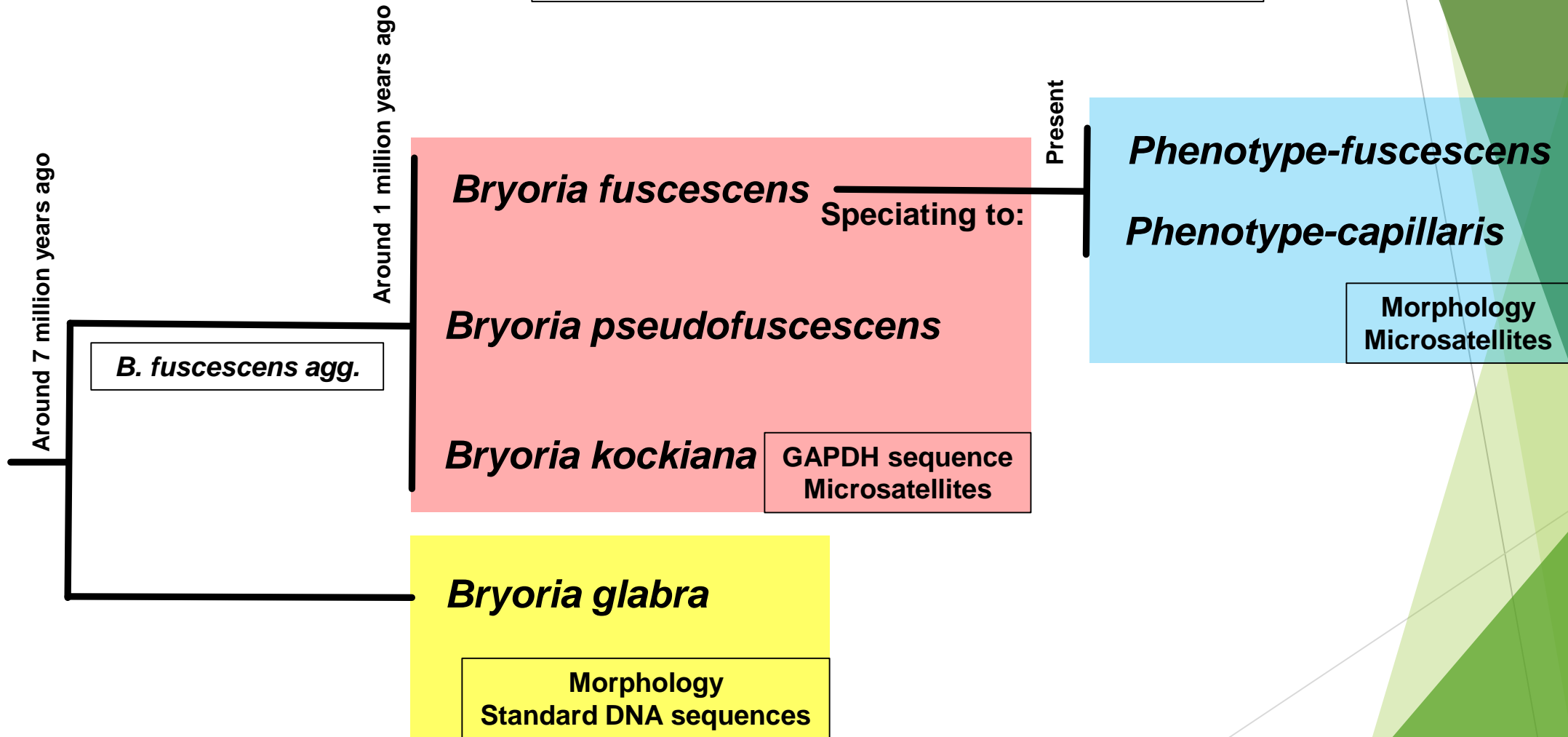


ML & Bayesian phylogenetic reconstruction of intergenic loci FRBi15 & FRBi16

Evidence of recombination

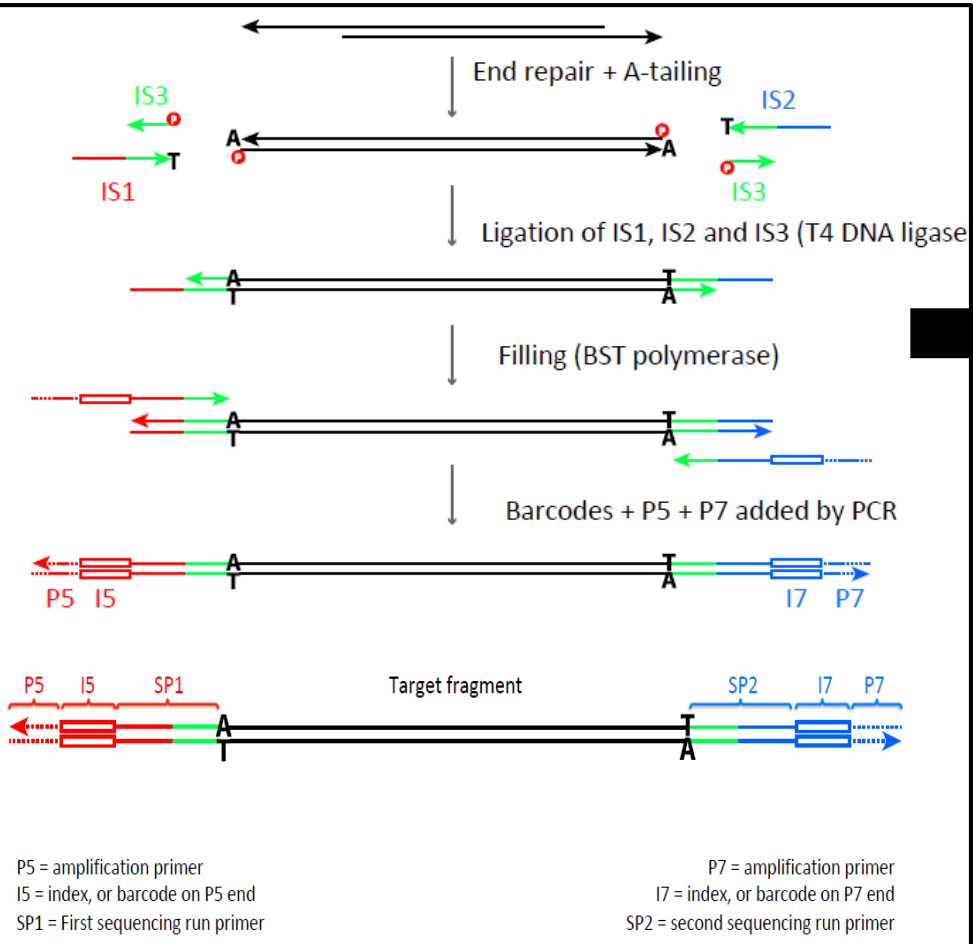
# Evolution of *Bryoria fuscescens*

## Evolutionary conclusions

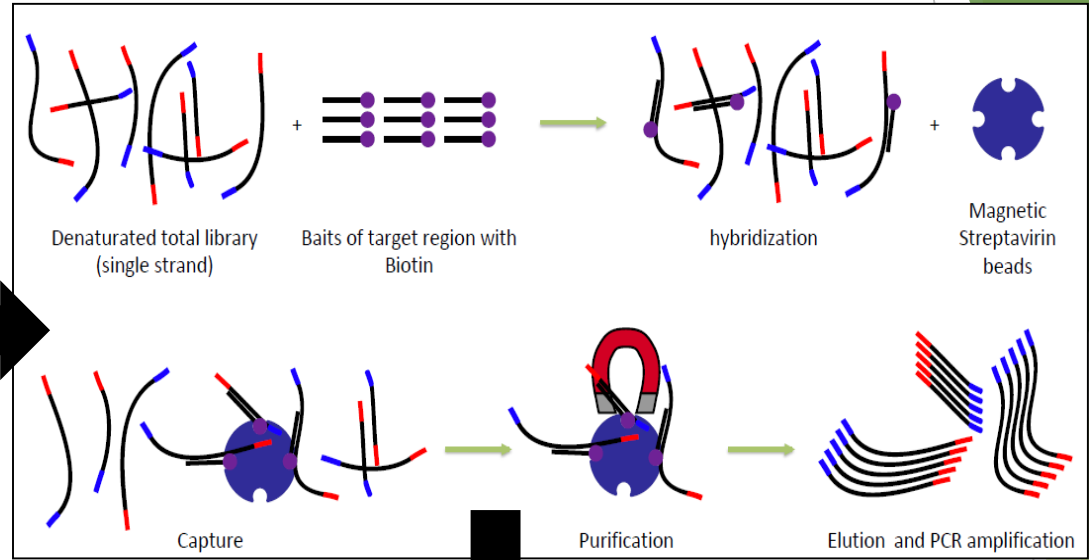


# Postdoctoral Research

## Library construction



## Gene Capture



760 plastidial and mitochondrial genomes  
1200 nuclear genes per specimen



# !Muchas gracias!



David L. Hawksworth



Víctor J. Rico



Christoph Scheidegger



Ana Crespo



GOBIERNO  
DE ESPAÑA

MINISTERIO  
DE ECONOMÍA  
Y COMPETITIVIDAD