Evolution of specificity within the lichen-forming genus *Peltigera* and its cyanobacterial partner: Consequences on speciation rate and geographical range

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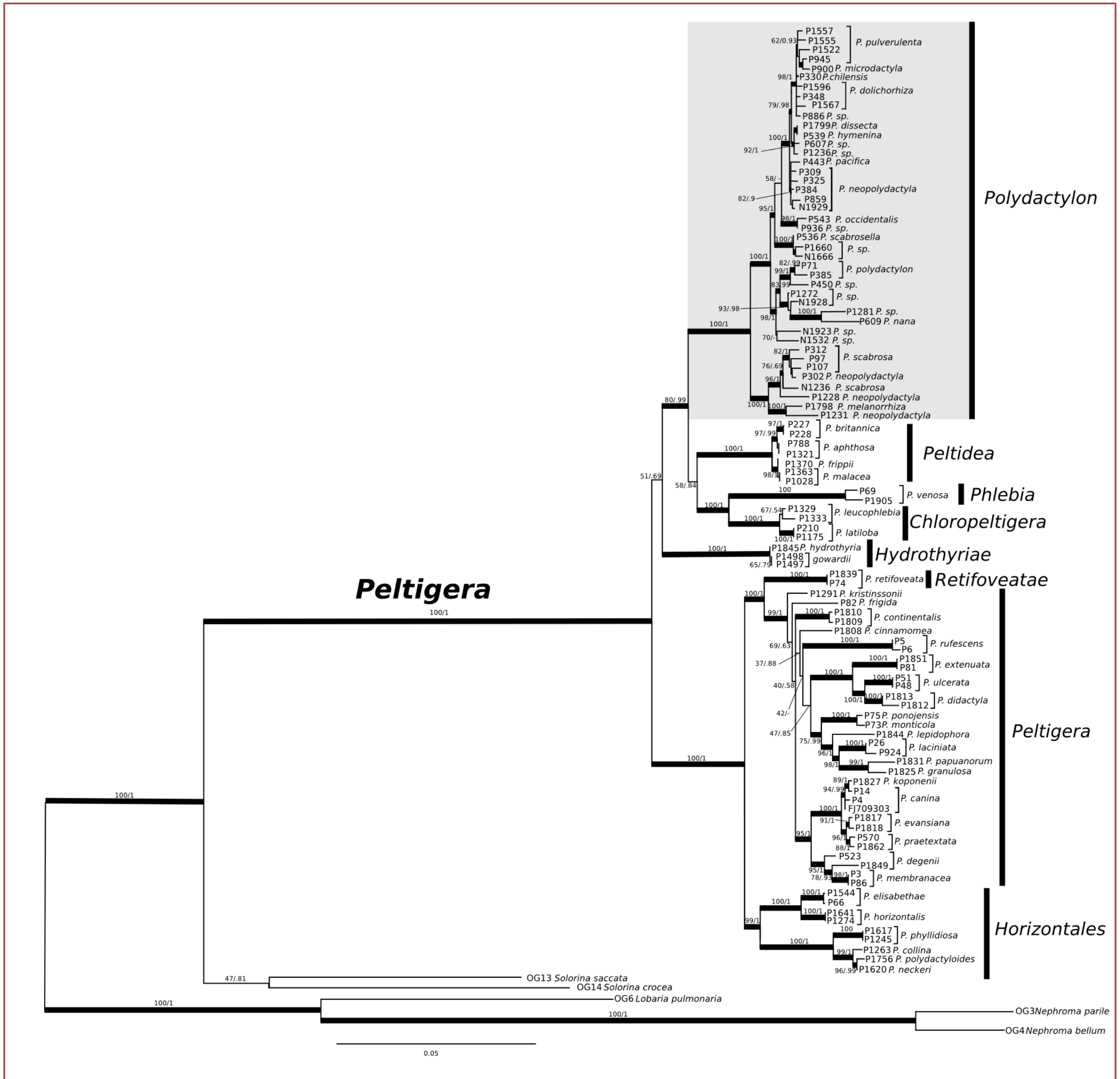
Peltigera section *Polydactylon*

- Monophyletic group of species
- Symbiosis involving an ascomycete fungus (*Peltigera*; mycobiont) and a cyanobacterium (*Nostoc;* cyanobiont)
- Group comprising species with different ecology and distributions (cosmopolitan, boreal, tropical, endemics…)

Phylogeny of the genus *Peltigera*



Aims of the study

1) Infer the phylogenetic relationships of both partners

2) Assess the specificity of both symbionts

3) Identify factors associated with specificity (geographic range, speciation rates, time, genetic diversity…)

*Consider these results in light of various hypotheses of evolution of mutualism

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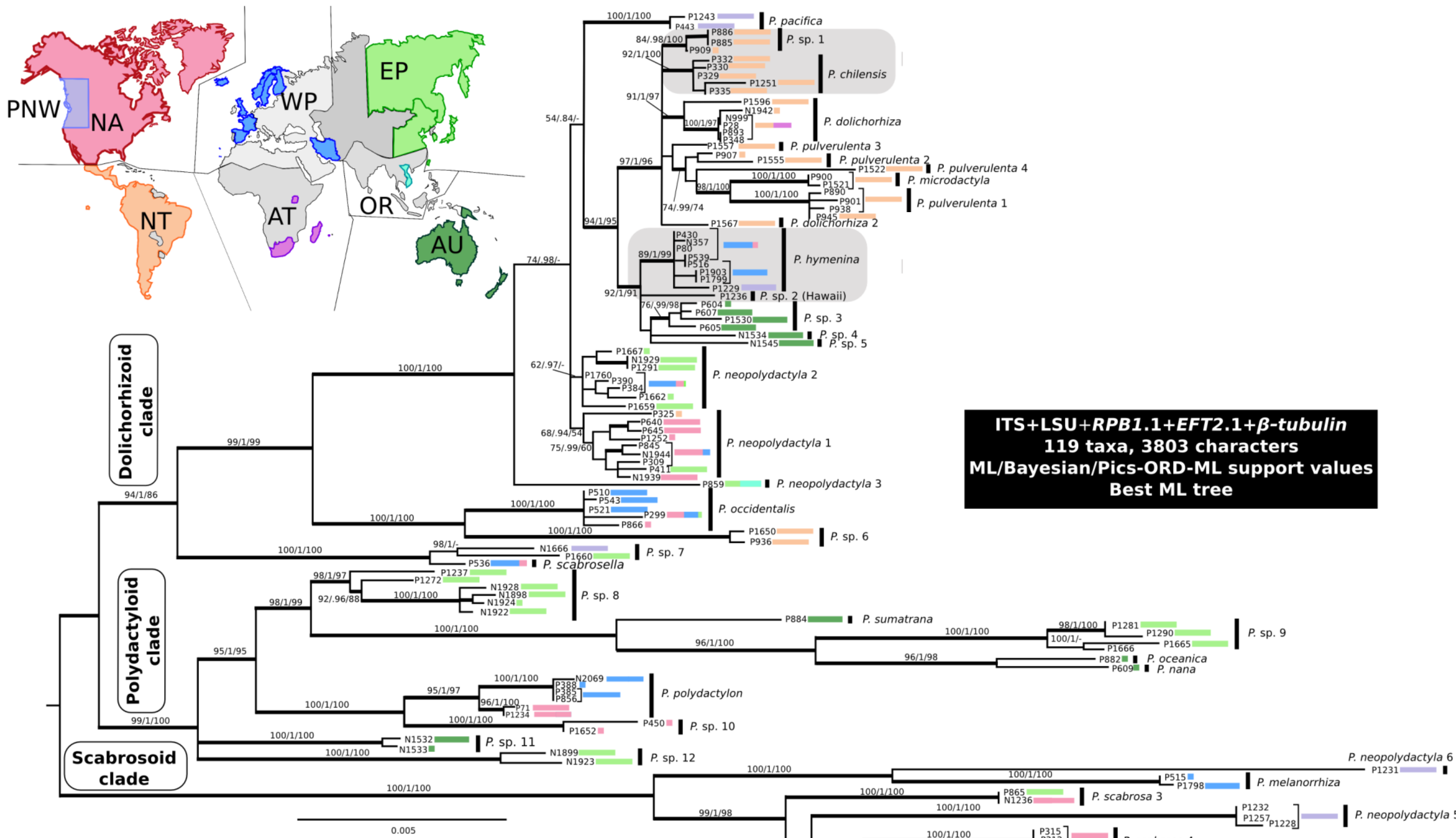
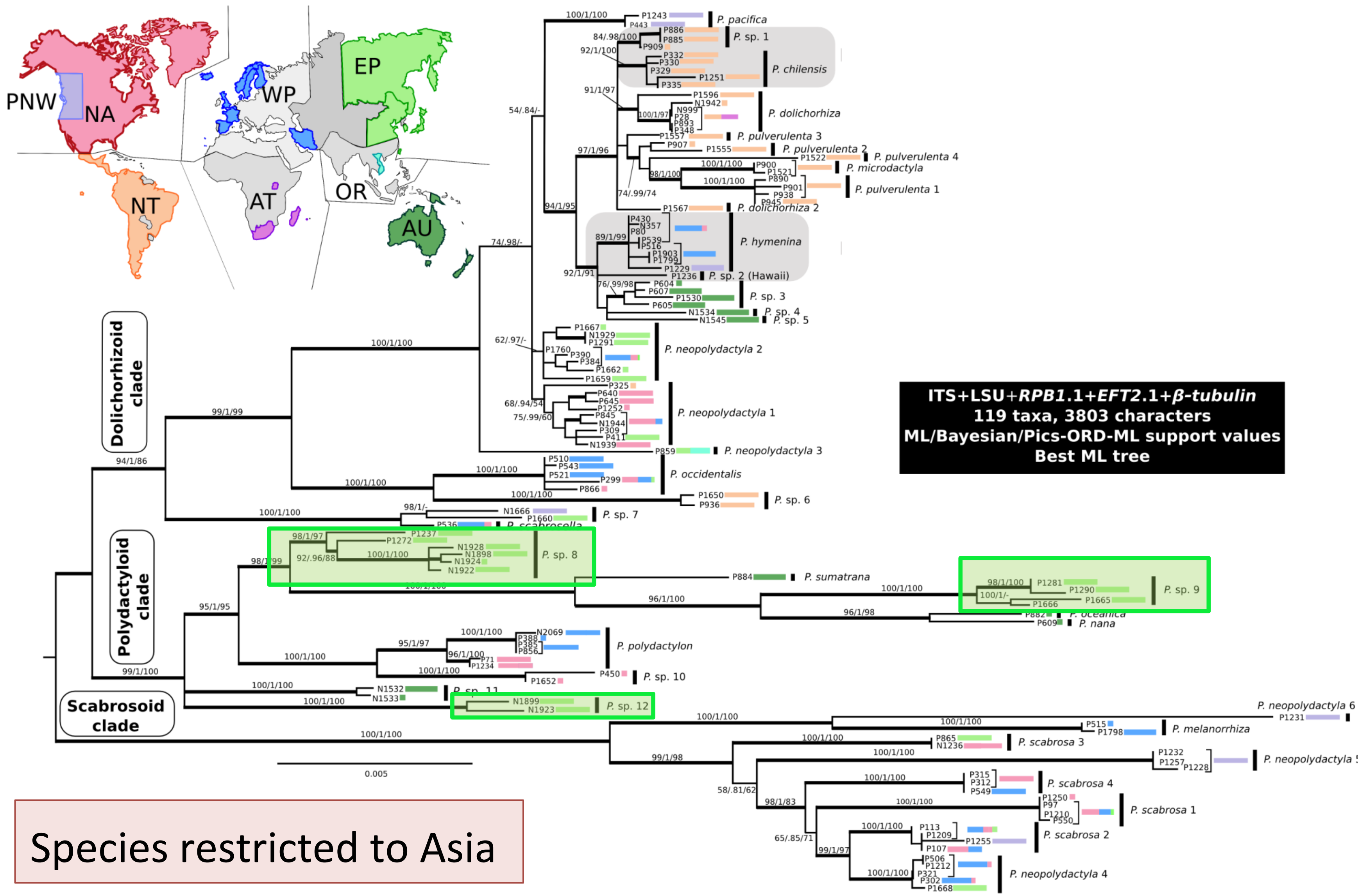
1a. Phylogeny of the mycobiont (*Peltigera*)



39 putative species

1a. Phylogeny of the mycobiont (*Peltigera*)



Species restricted to Asia

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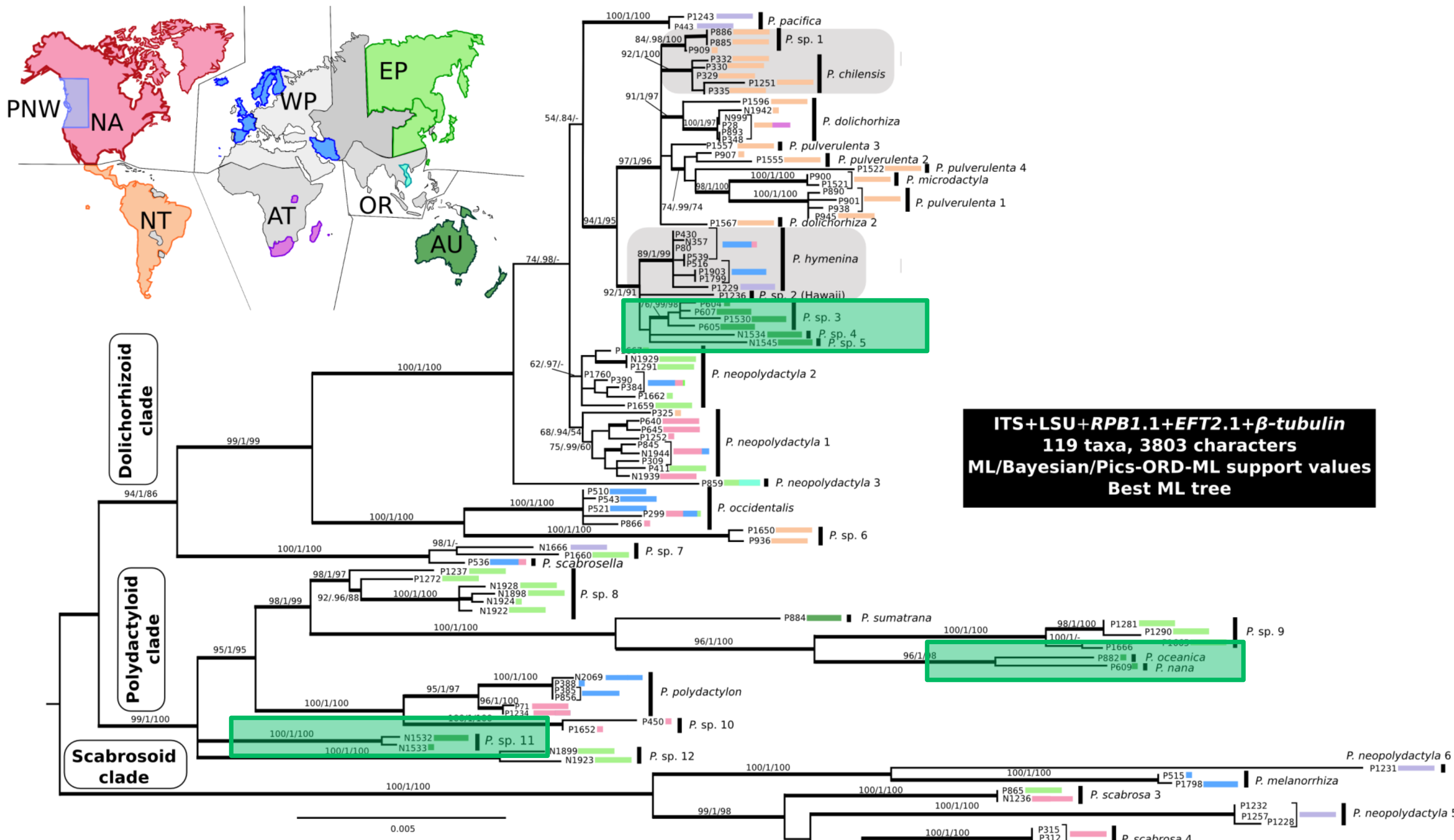

Species restricted to Australasia

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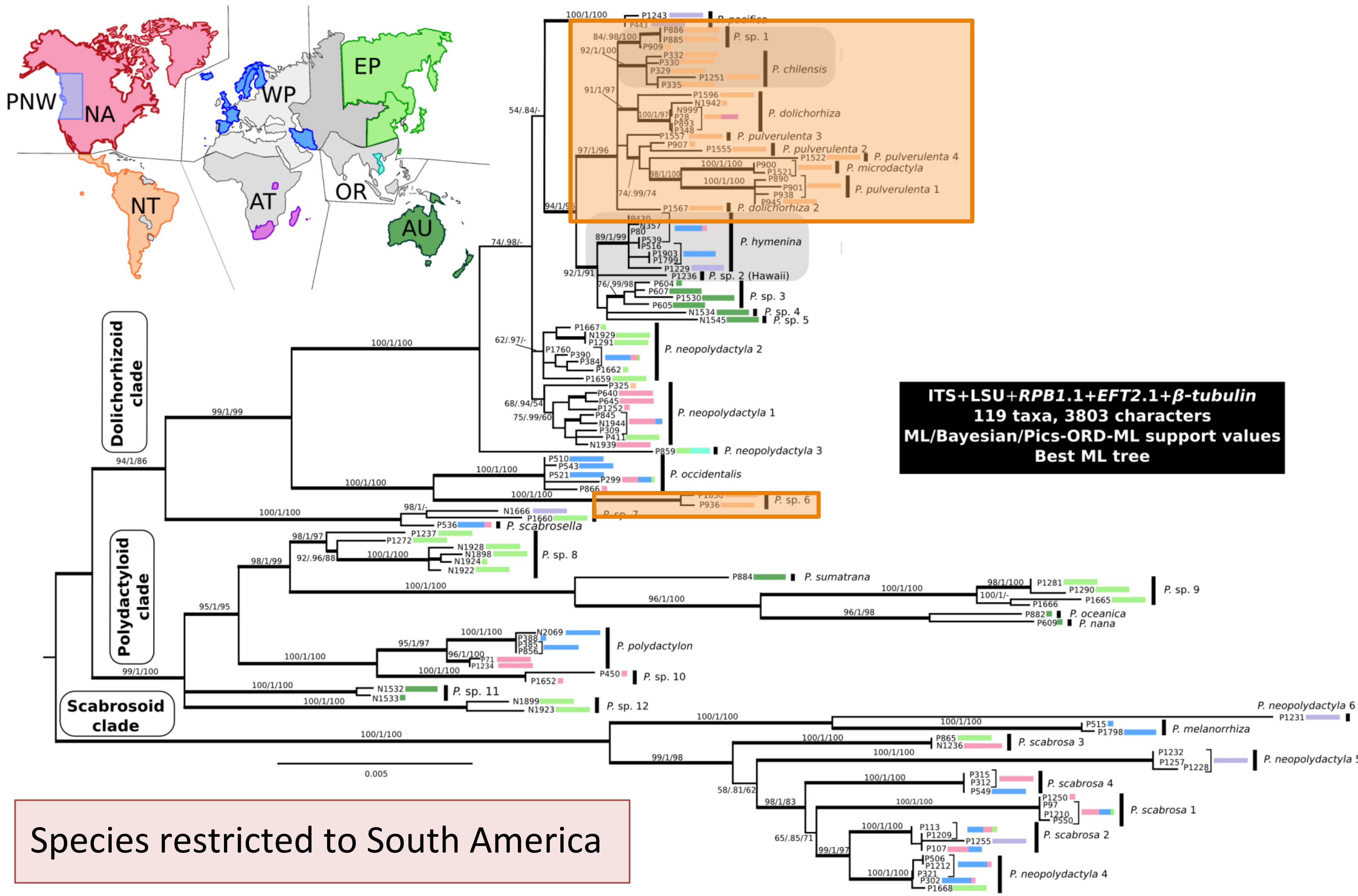

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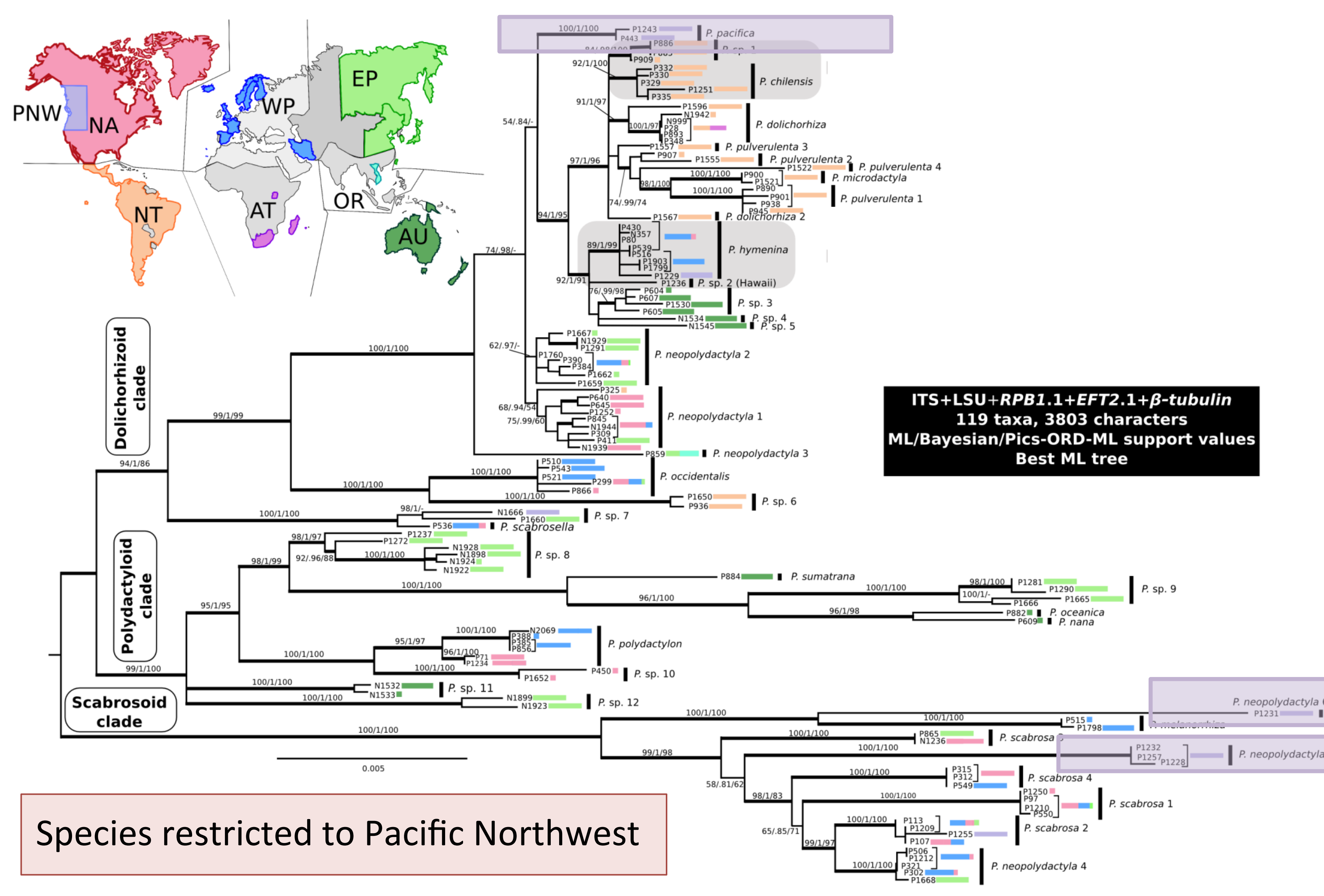

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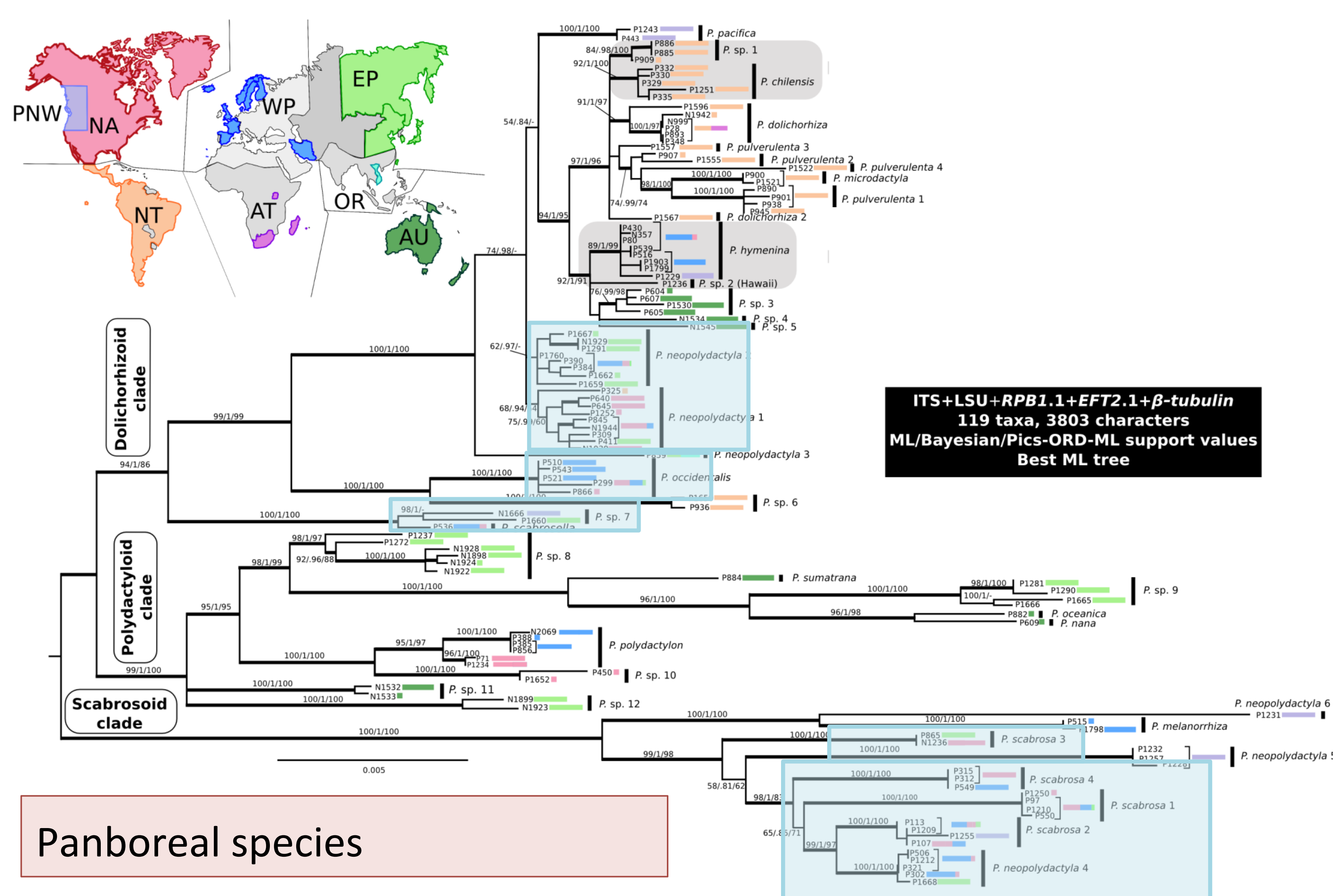

Panboreal species

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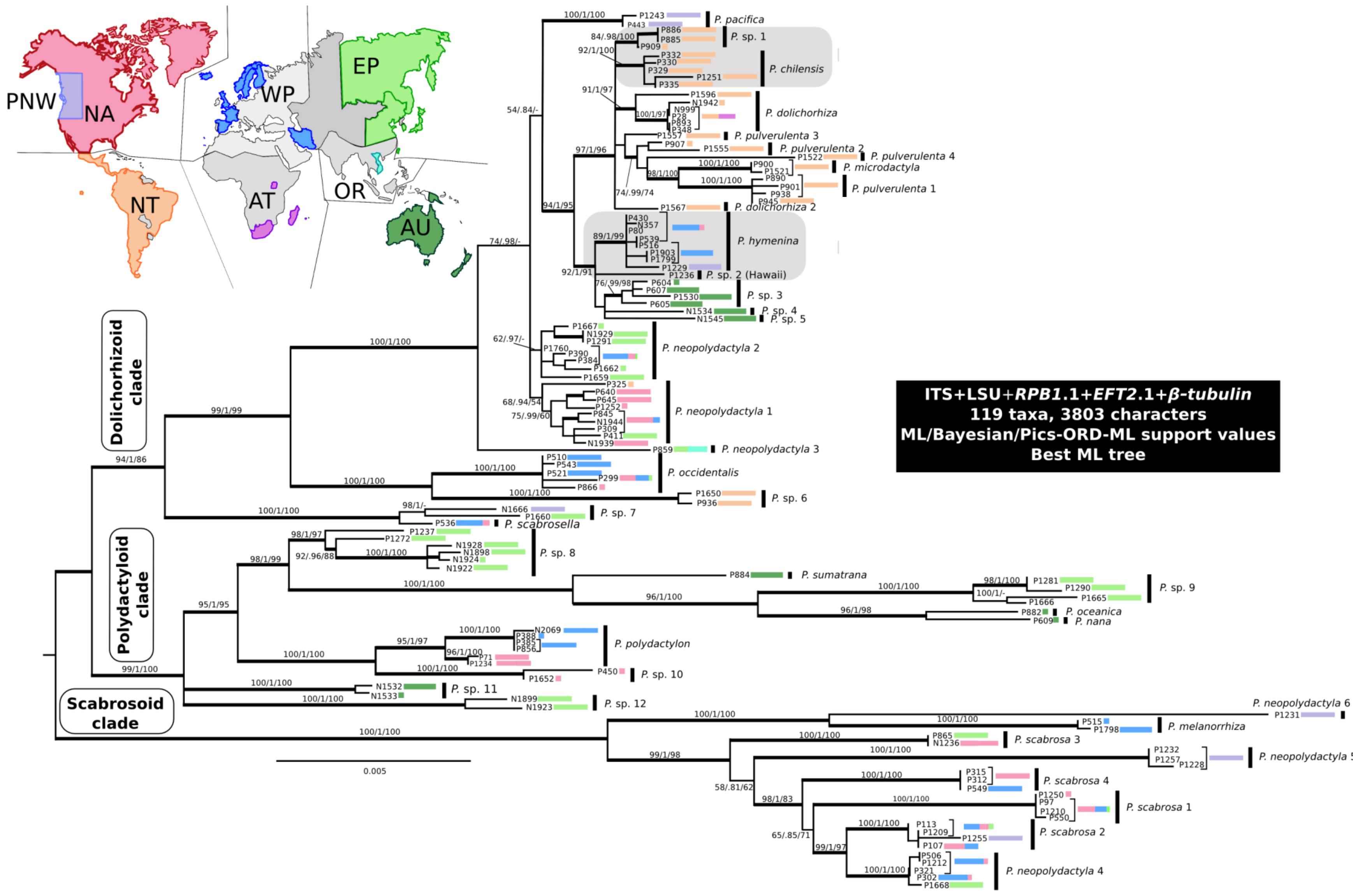
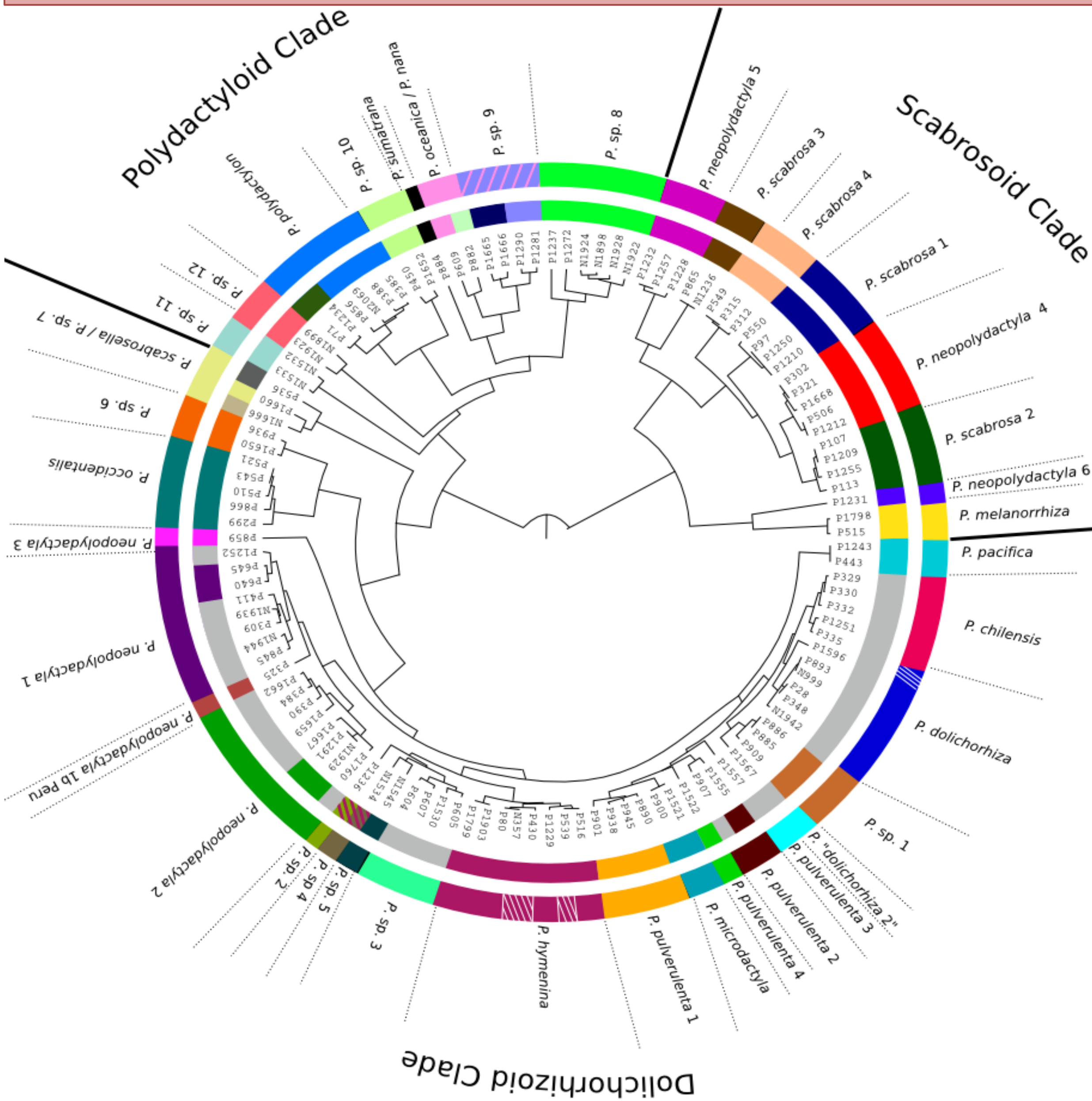
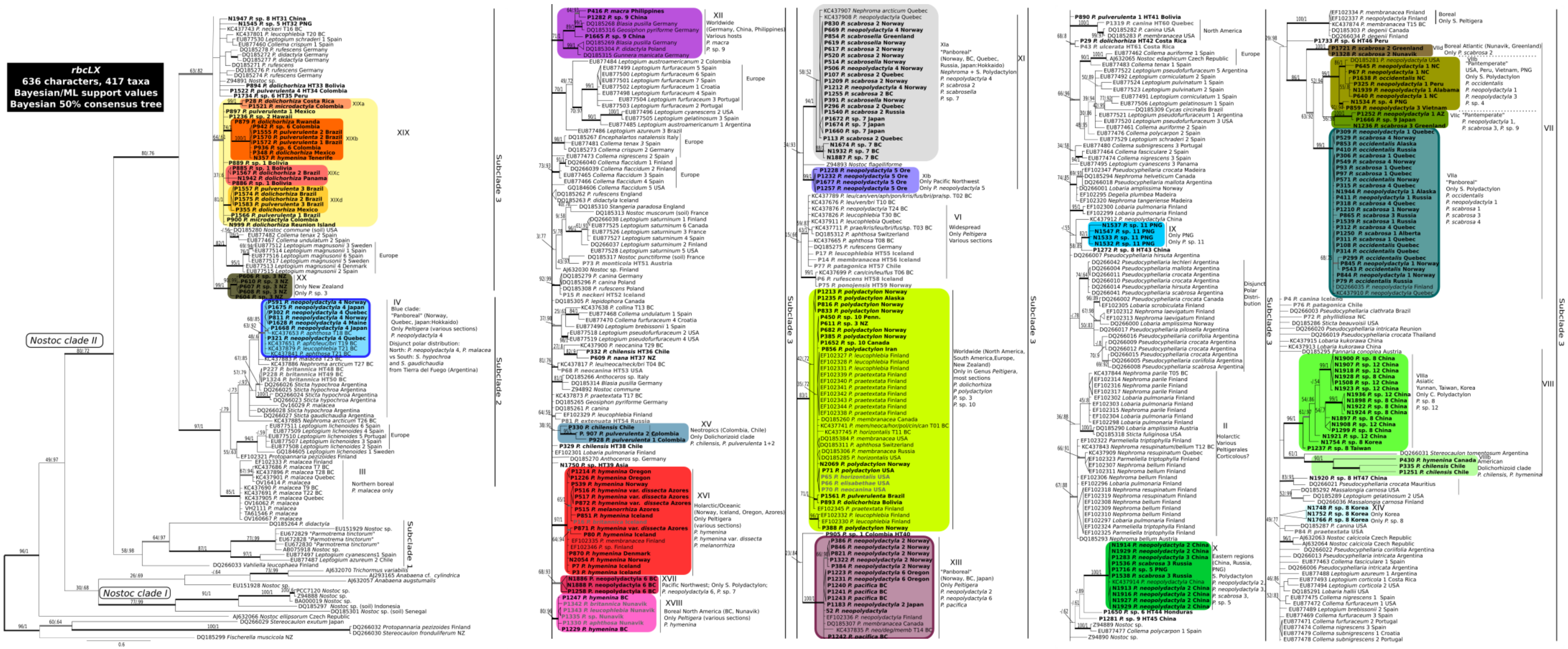


2a. Species delimitation (discovery)



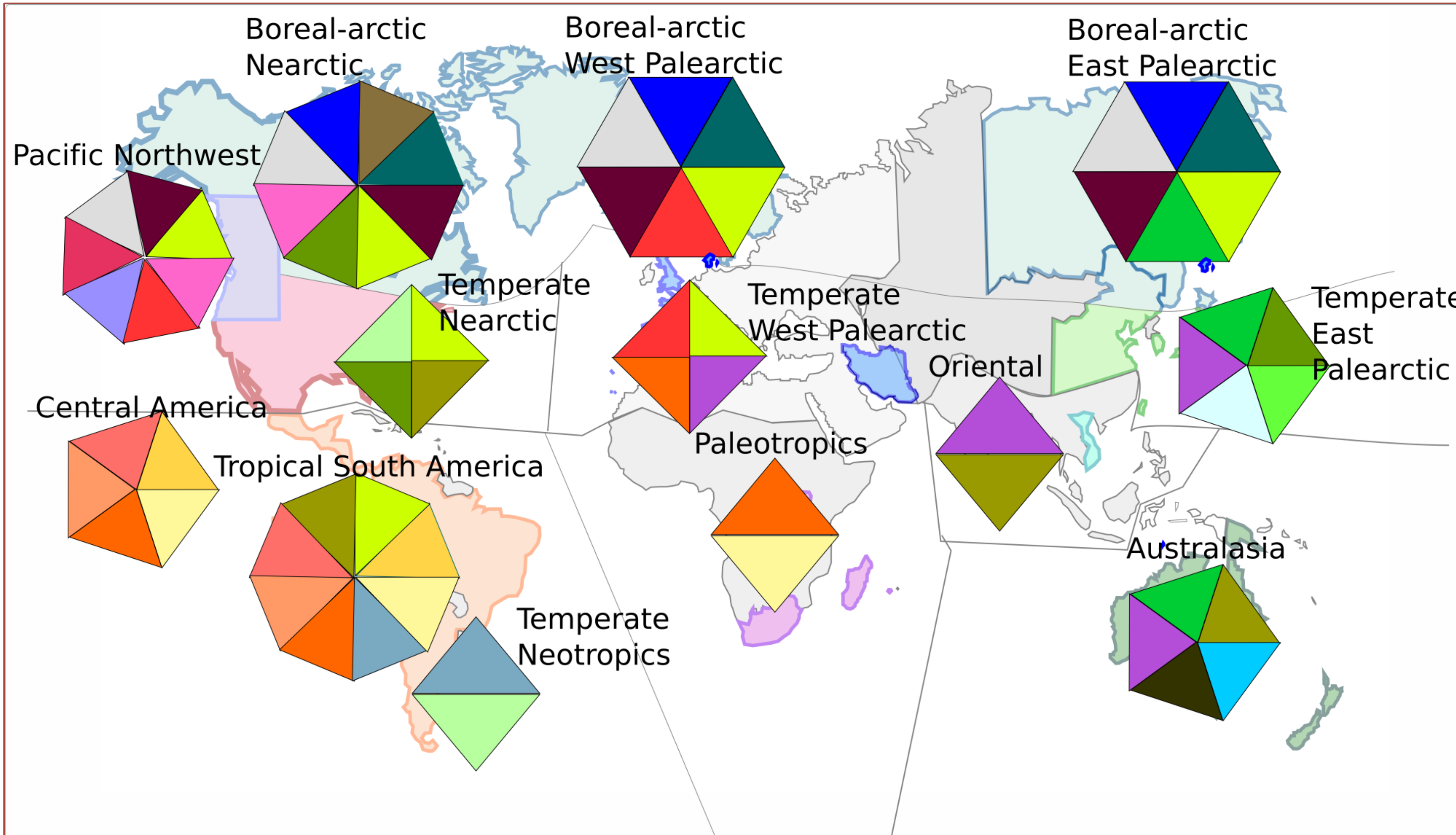
- 2 methods: Structurama (all loci) and bGMYC (ITS)
- Attribute a « species proxy » to the samples used in the analyses

1b. Global *rbcLX* phylogeny of *Nostoc*



- Delimitation of 25 phylogroups based on well-supported monophyletic groups of closely related *Nostoc*
- 18 associated only with section *Polydactylon*, 22 only with *Peltigera* => specificity

1c. Distribution of cyanobiont (*Nostoc)* phylogroups



Very strong climatic and geographic patterns in the *Nostoc* distribution

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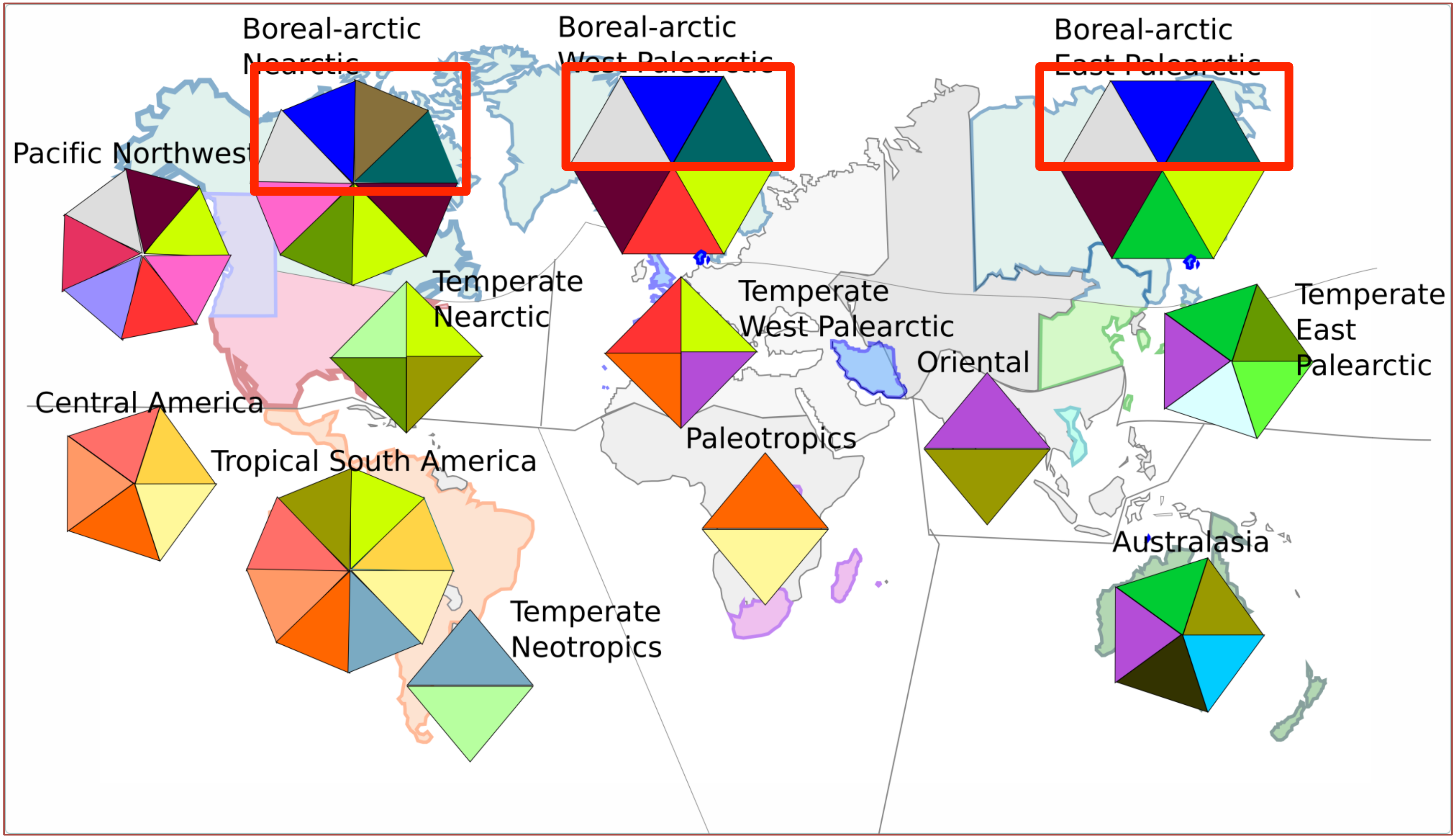

Boreal phylogroups

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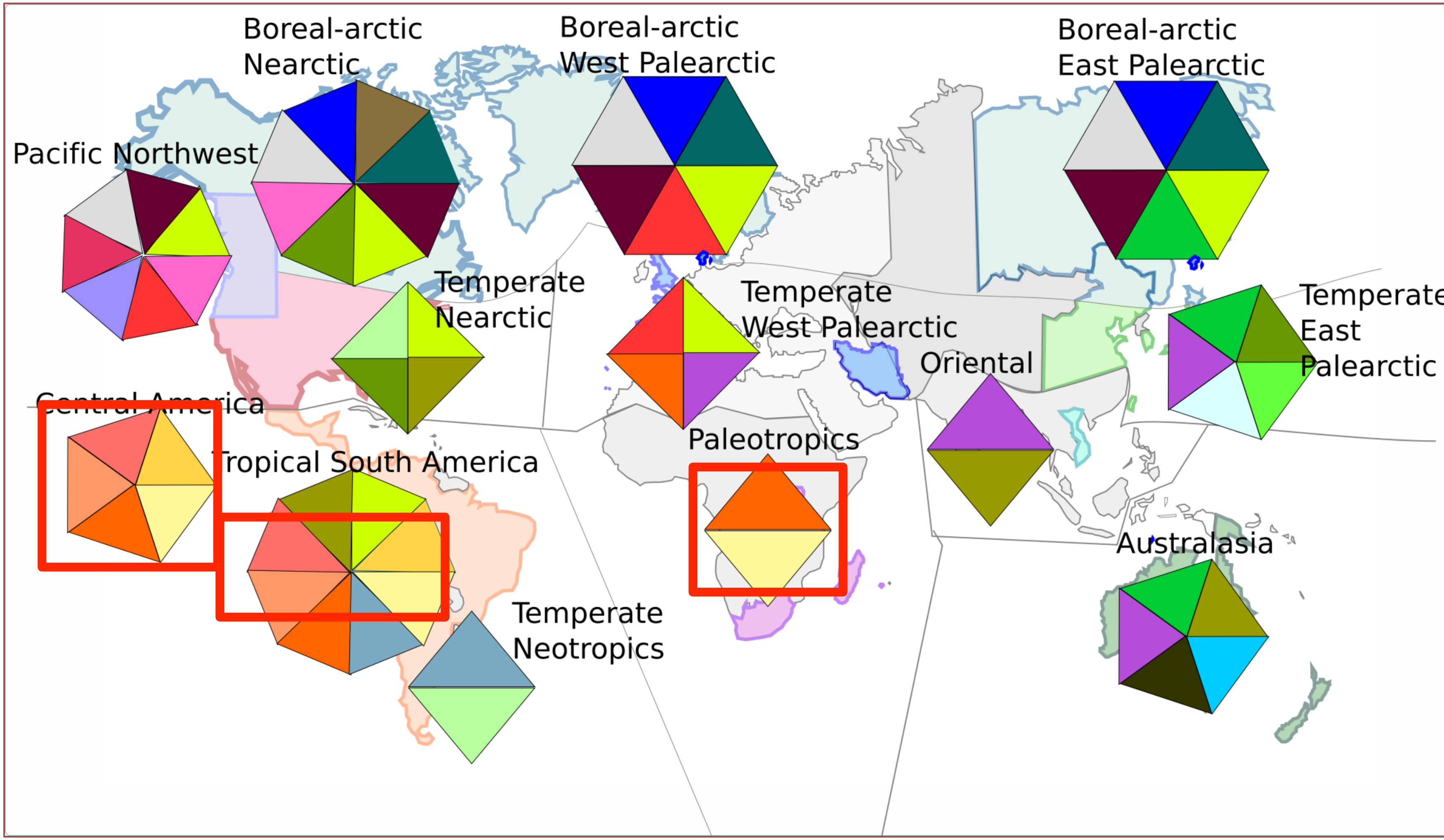

Tropical phylogroups

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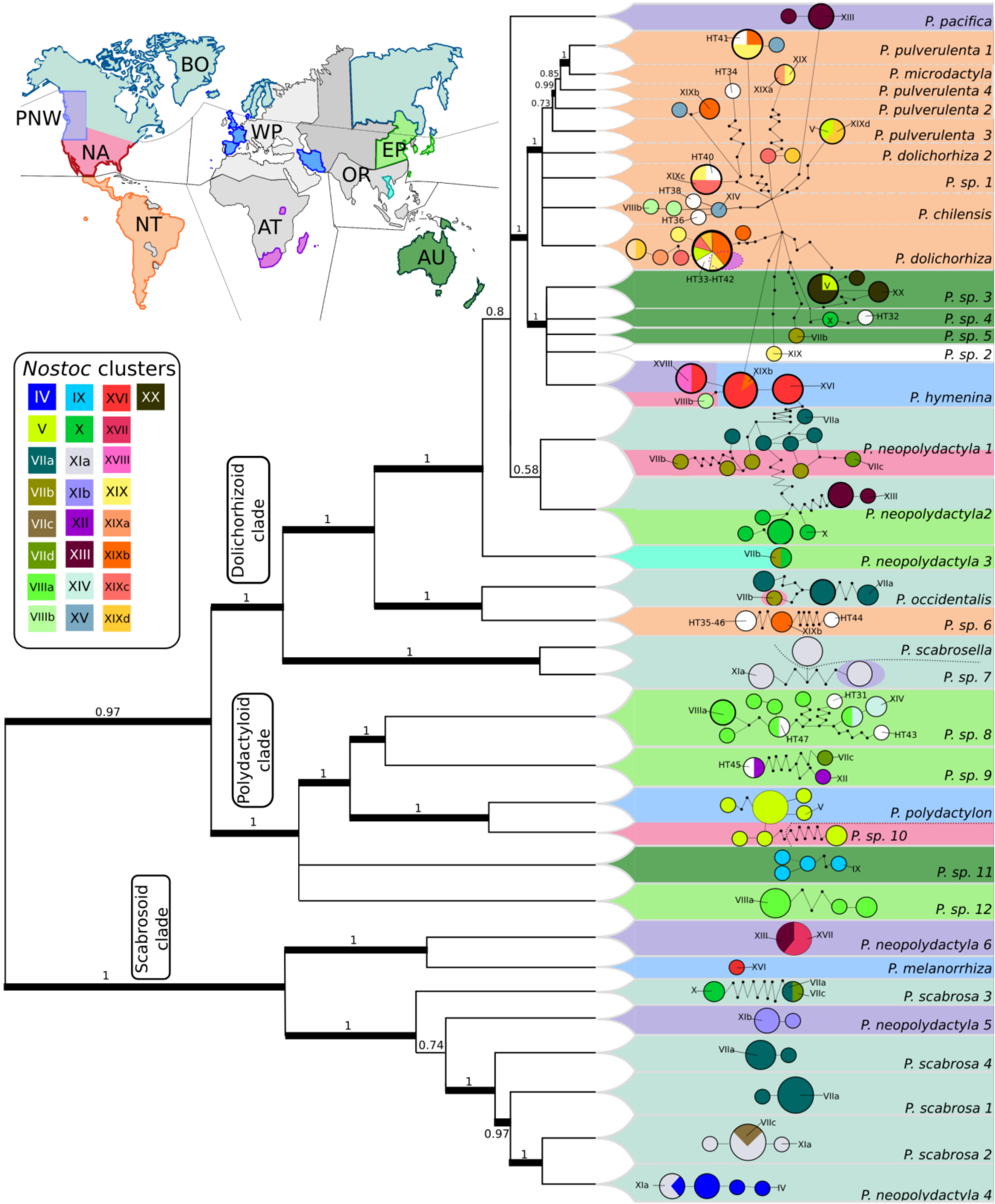
2b. Specificity of the symbionts

- Different mycobiont profiles, from strict specialist to generalist
- Cases of local mycobiont specialists with cyanobiont switches
- Possible influence of time, with old mycobiont specialist species and recent generalists
- Radiation of mycobiont correlated with generalism
- Mycobiont specialists have usually less haplotypes than generalists



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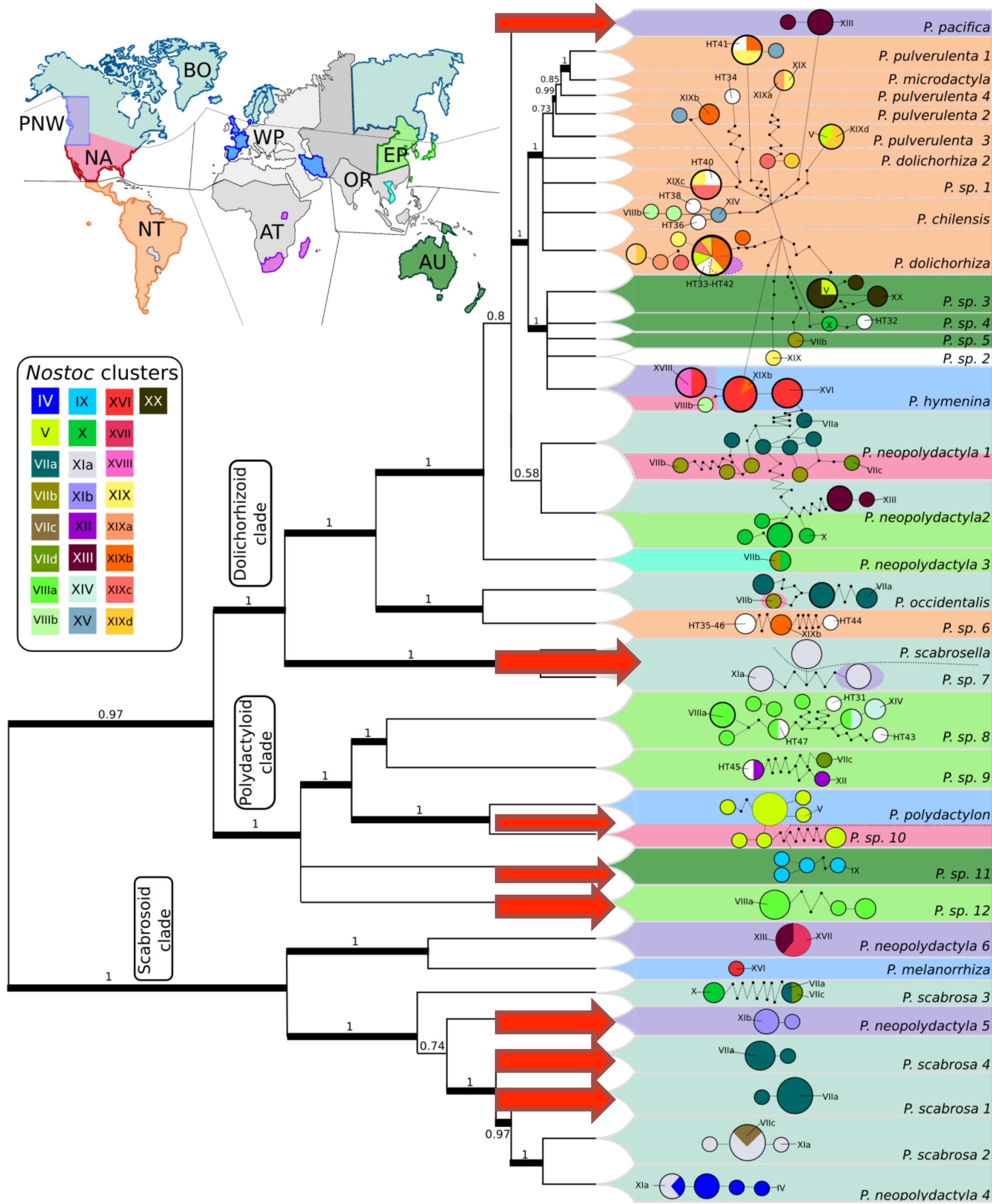

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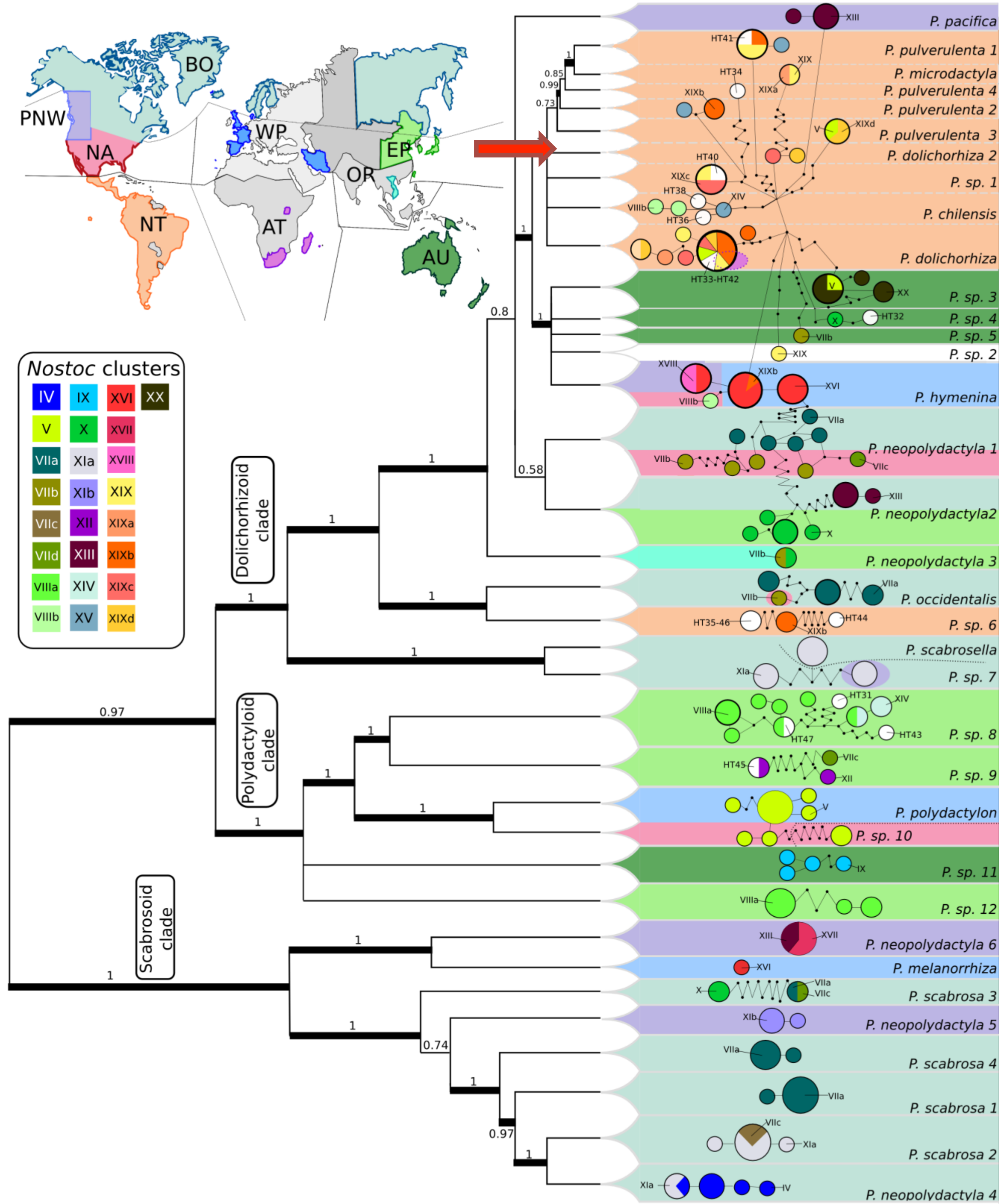

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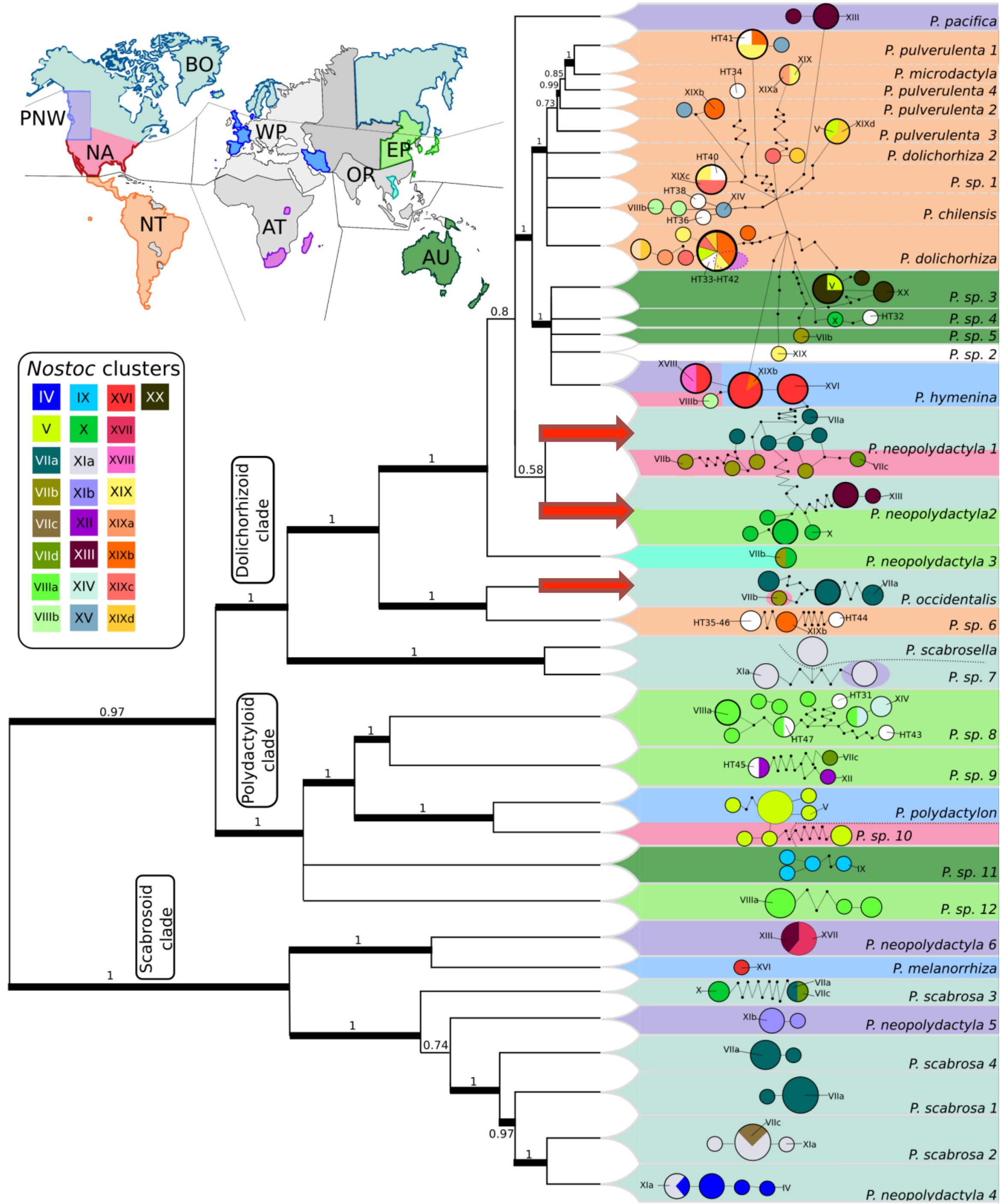
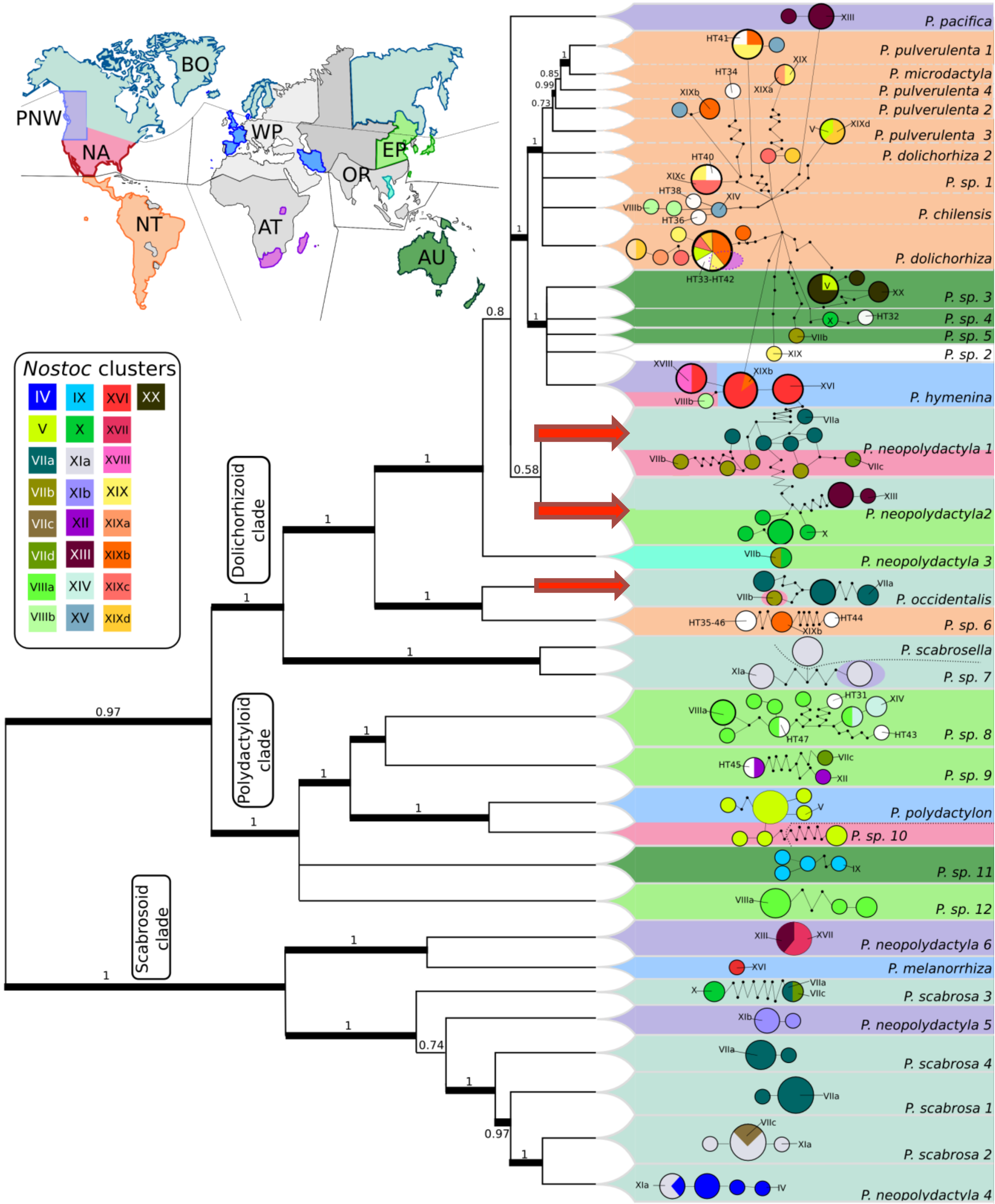


Geographic mosaic of coevolution theory (Thompson)

- A species may adapt and become specialized to another species differently in separate regions
- Long-term dynamics of coevolution may occur over large geographic ranges rather than within local populations



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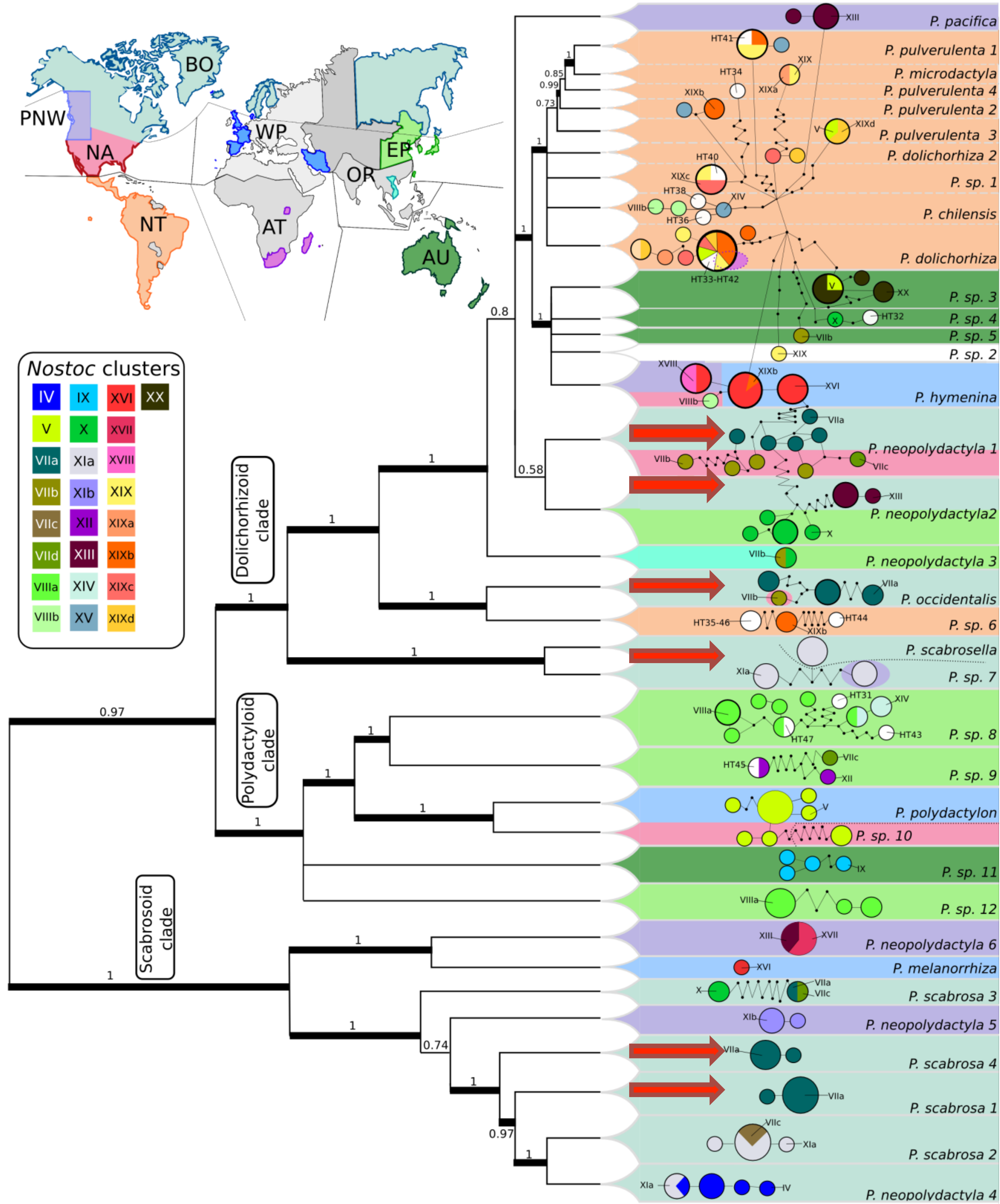

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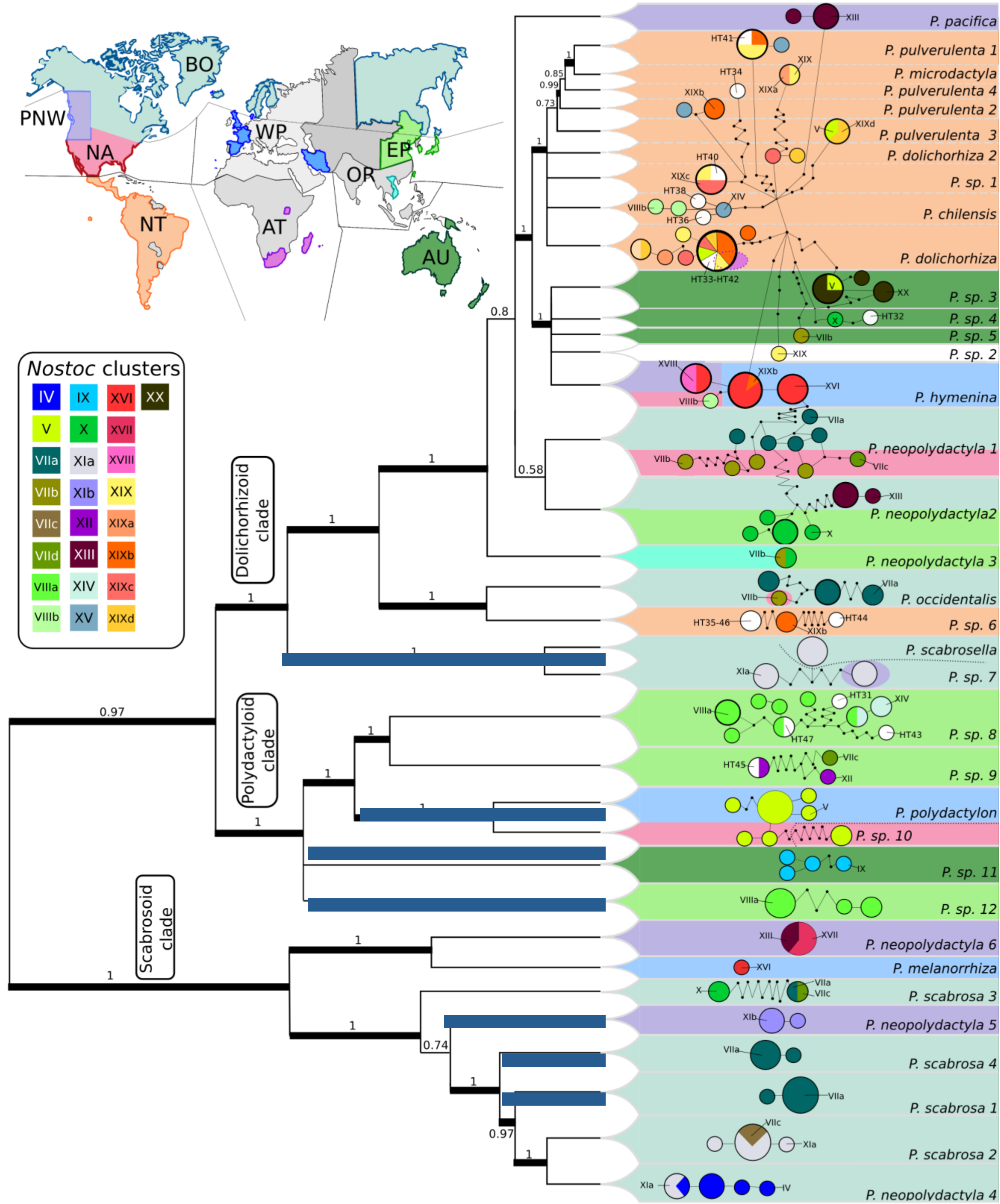

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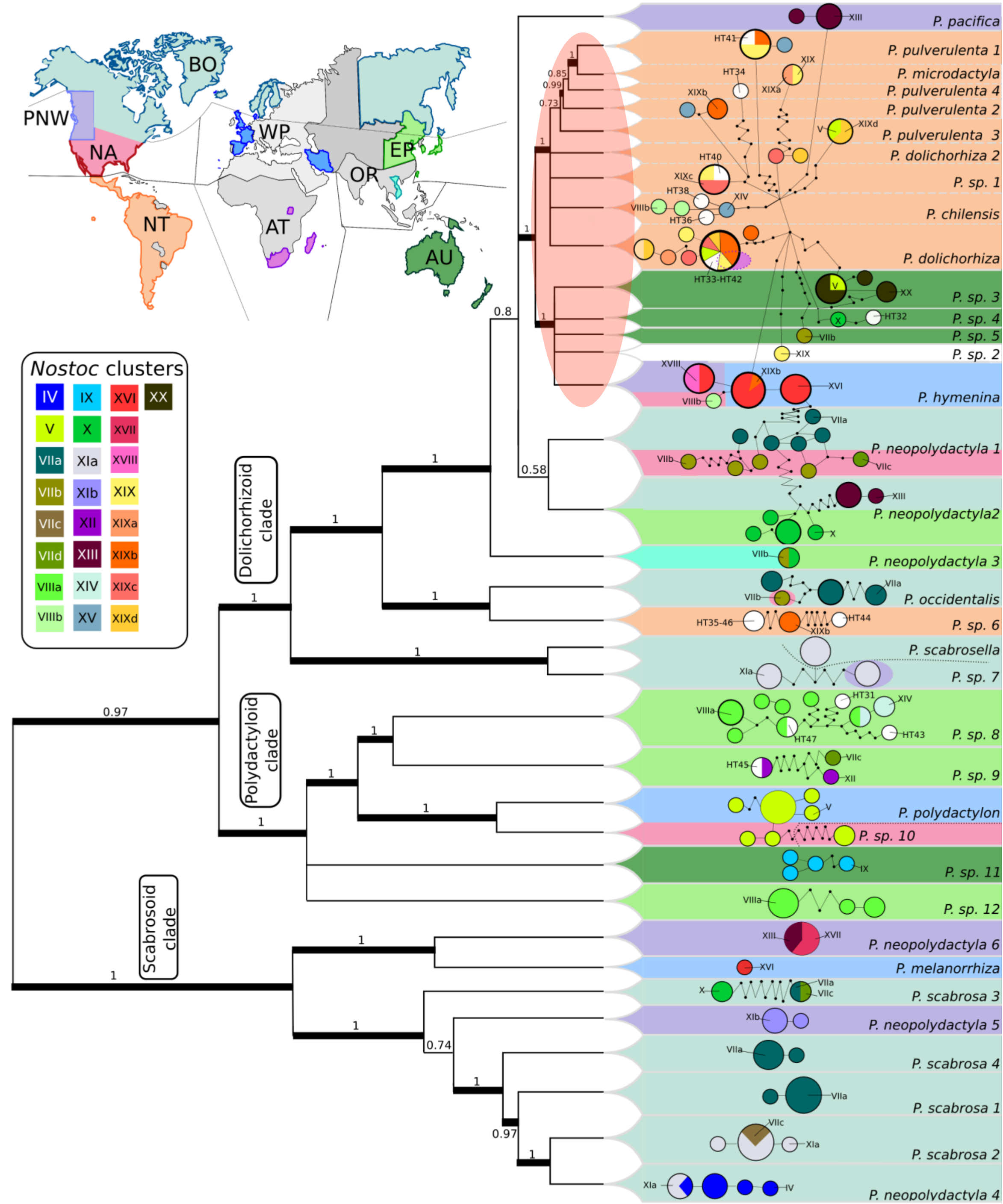

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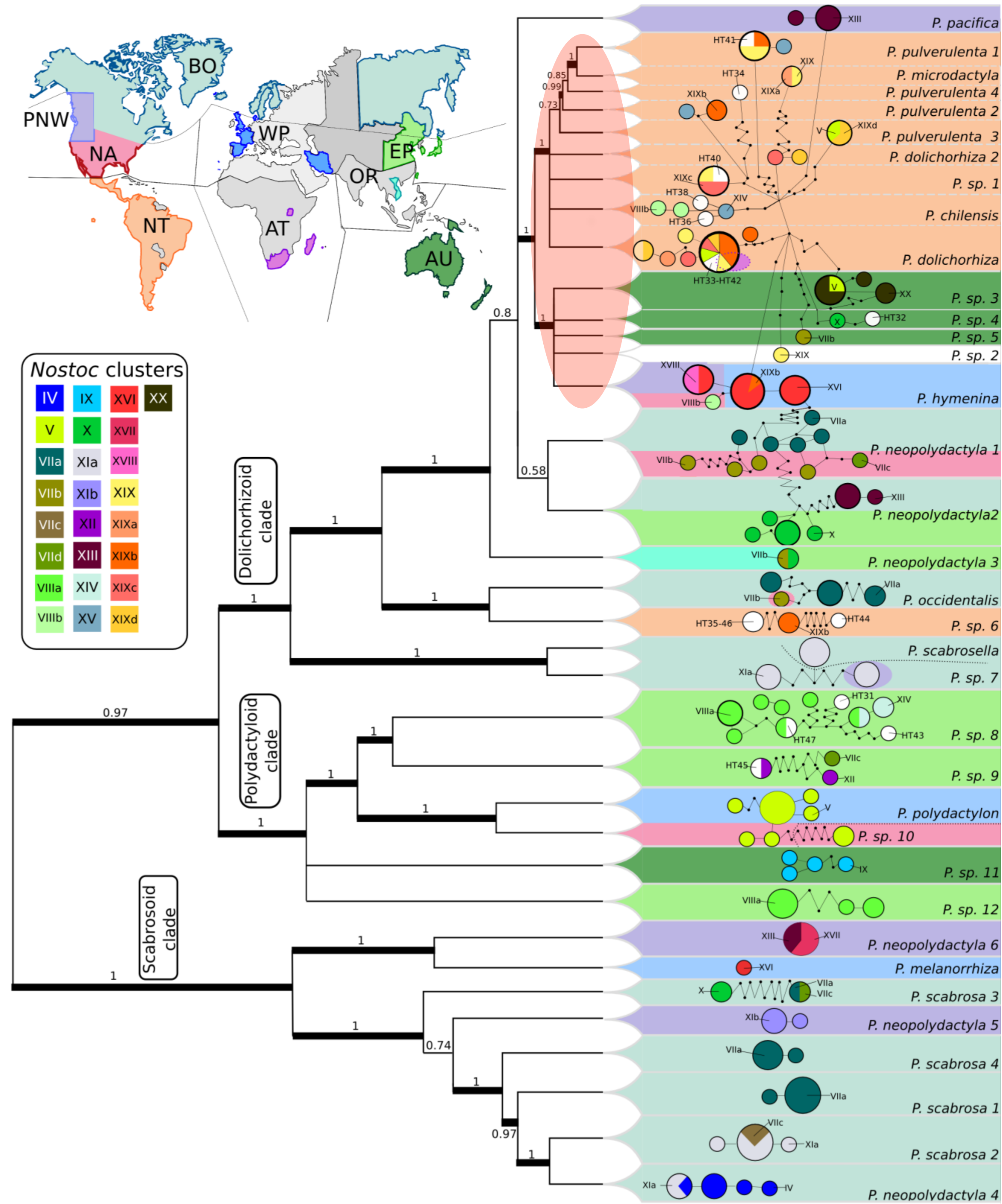

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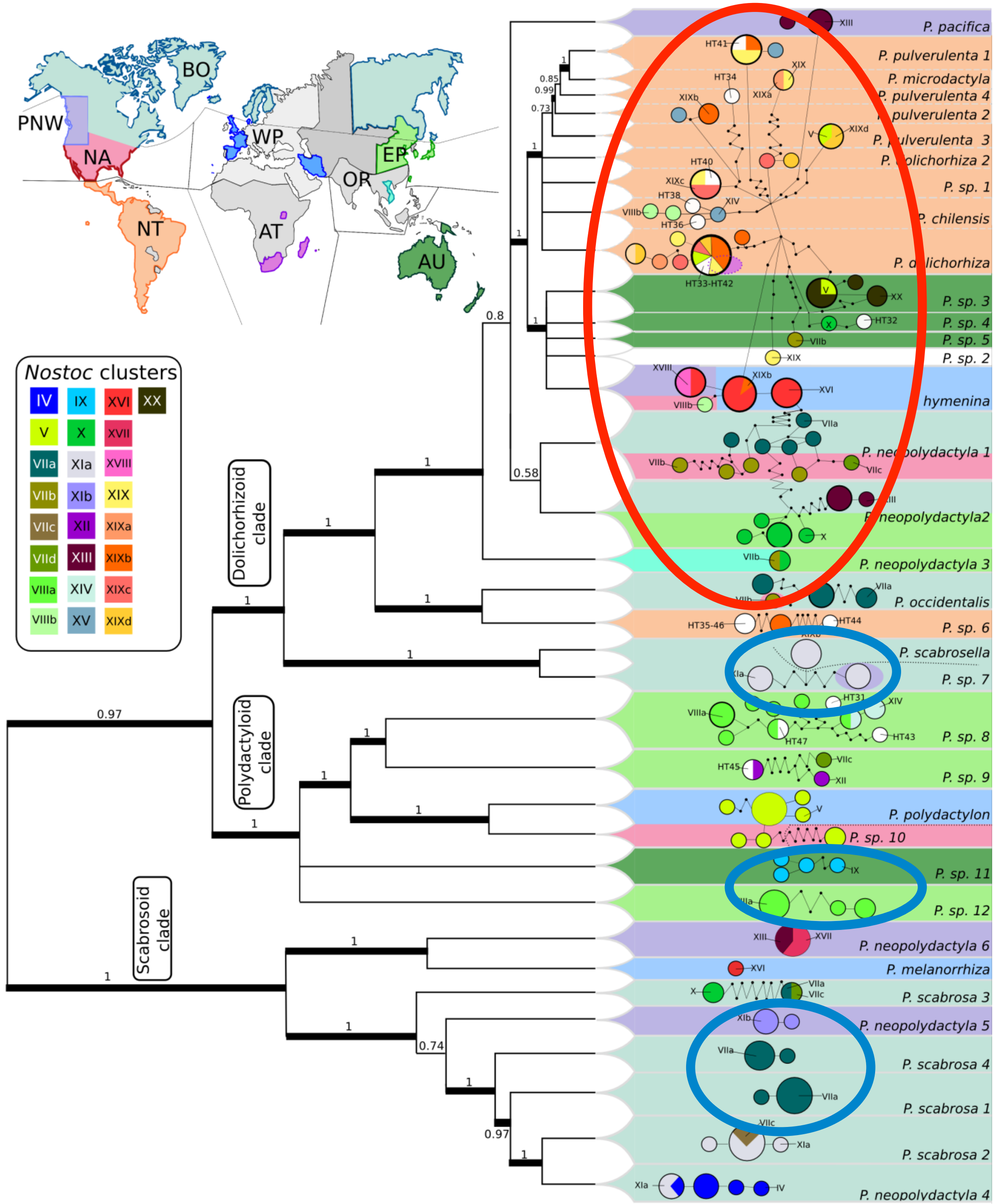

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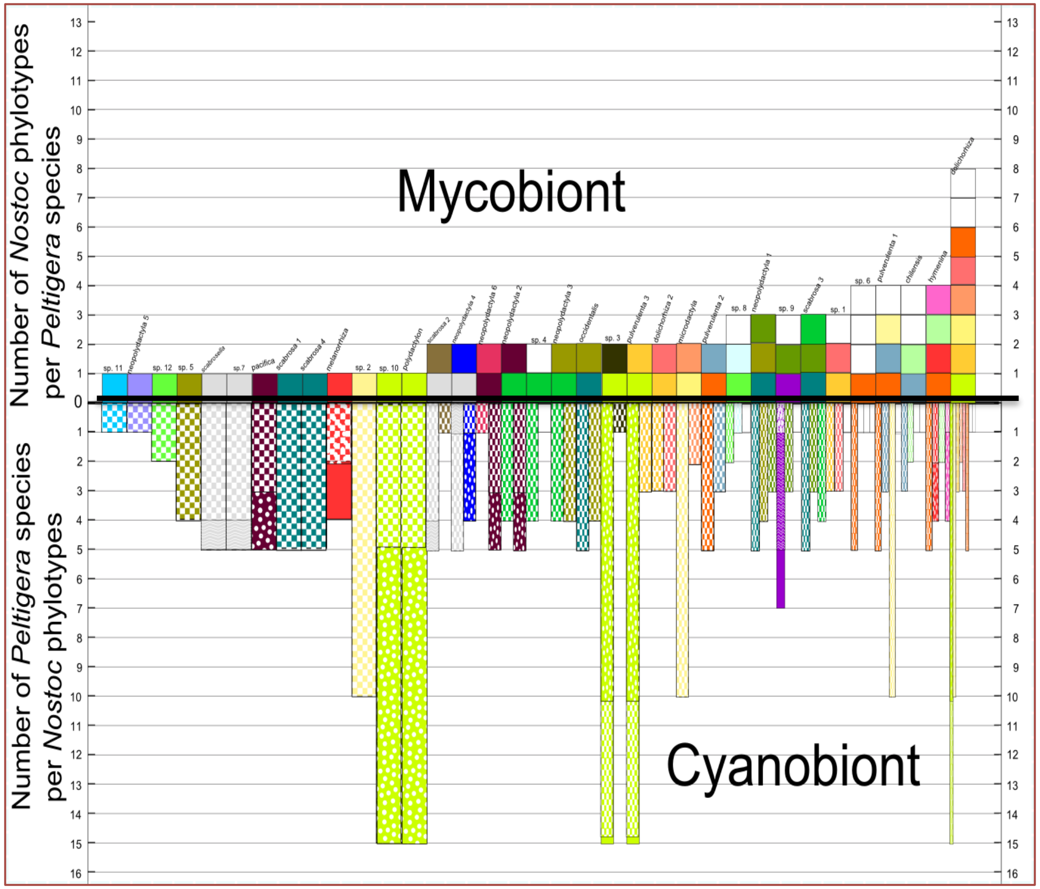

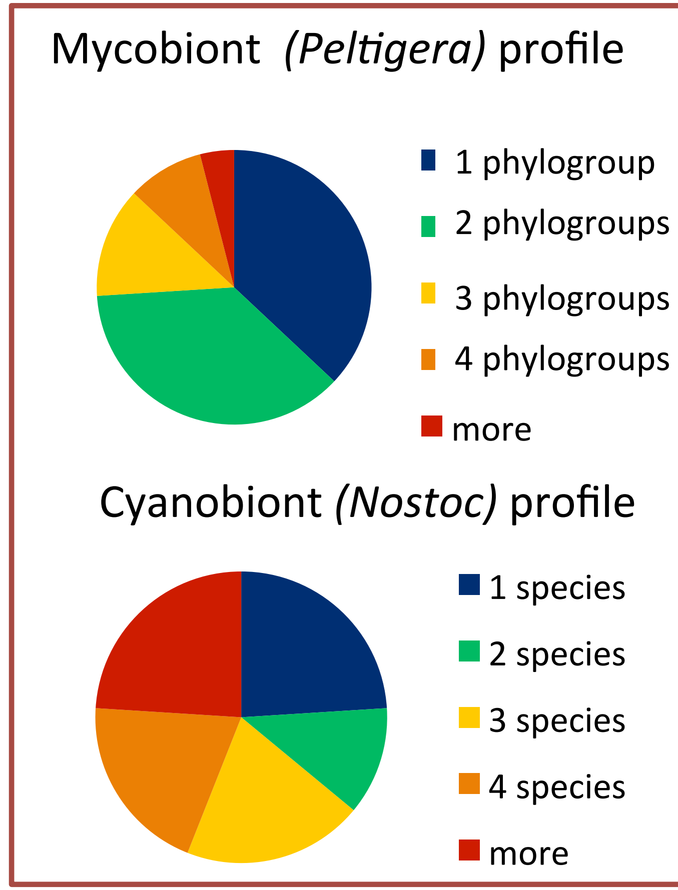

- In average, 2 phylogroups per *Peltigera* species, 3.4 species (of *Peltigera*) per *Nostoc* phylogroup.
- **The mycobiont is more specialized than the cyanobiont.**

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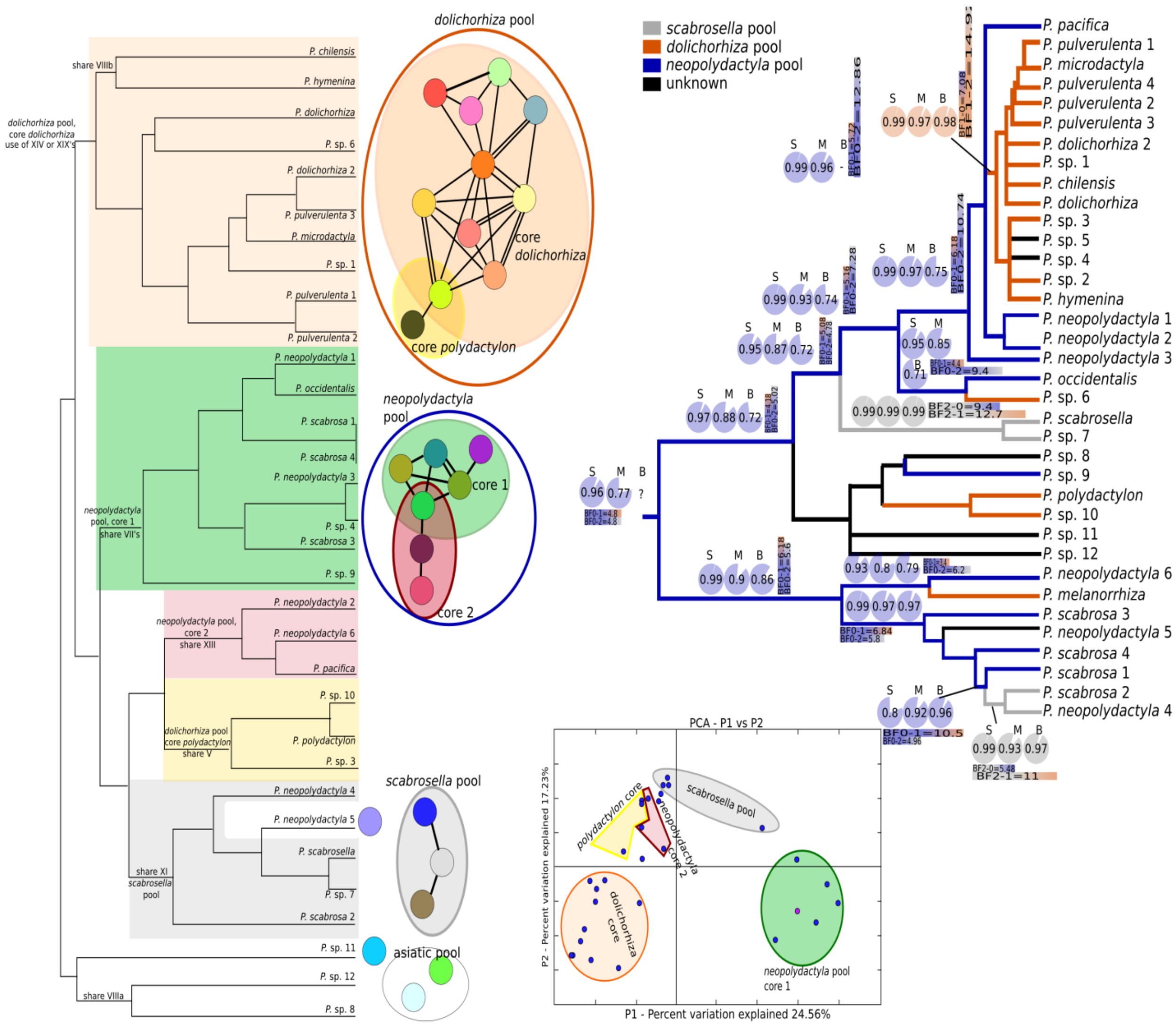
3a. Factors associated with specificity



- *Nostoc* pools shared by sets of mycobiont species (Uni Frac)
- Switches of *Nostoc* pools might be correlated with mycobiont expansion to new regions/ environments and/ or driving speciation
- Geographic mosaic of coevolution

3b. Impact of specialization on speciation rate

1) BiSSE: comparing specialists (1 *Nostoc* phylogroup only) and non-specialists *Peltigera* species:

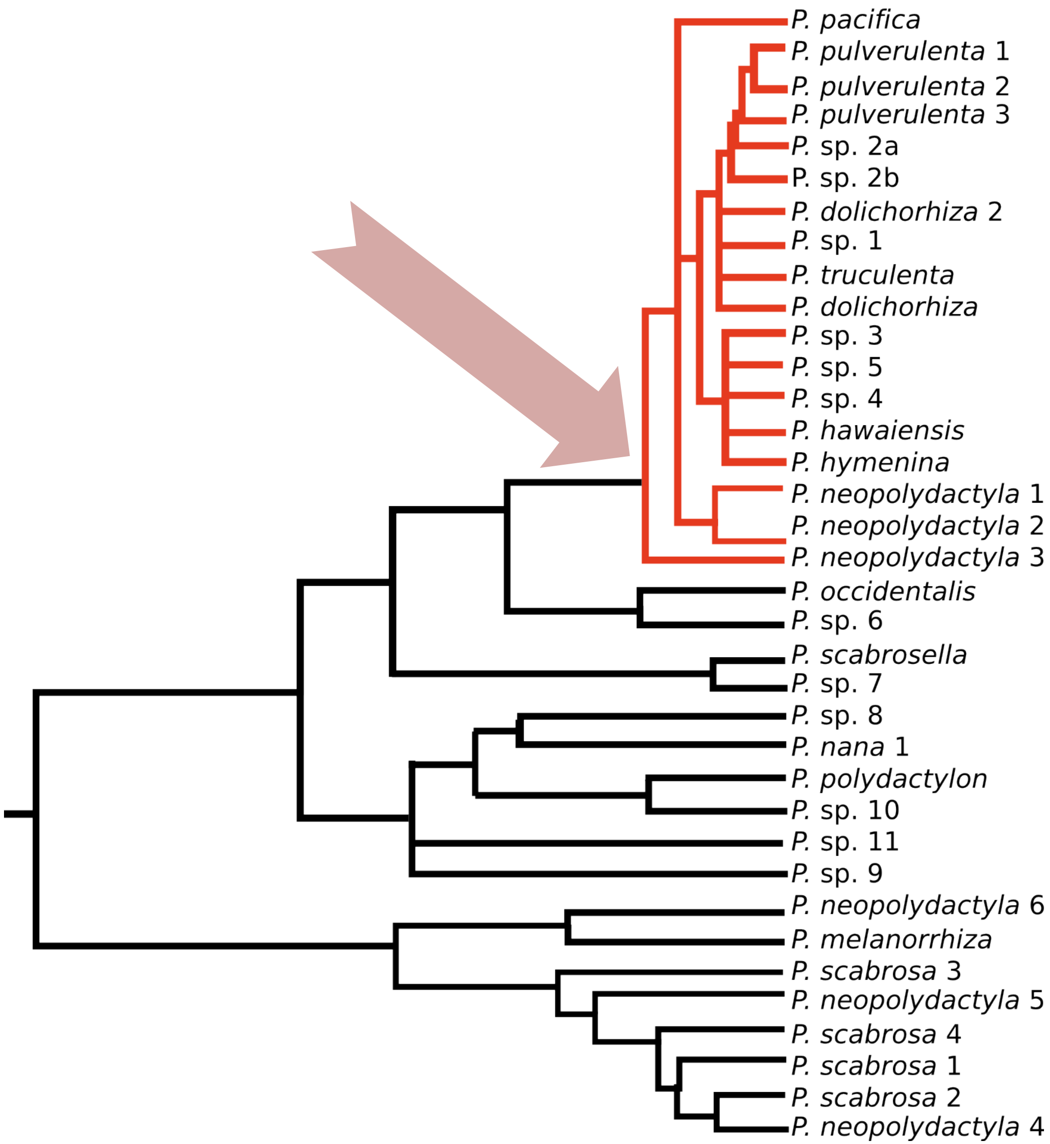
    a) speciation rates significantly higher in generalists

    b) switching rate generalist => specialist significantly higher than specialist => generalist

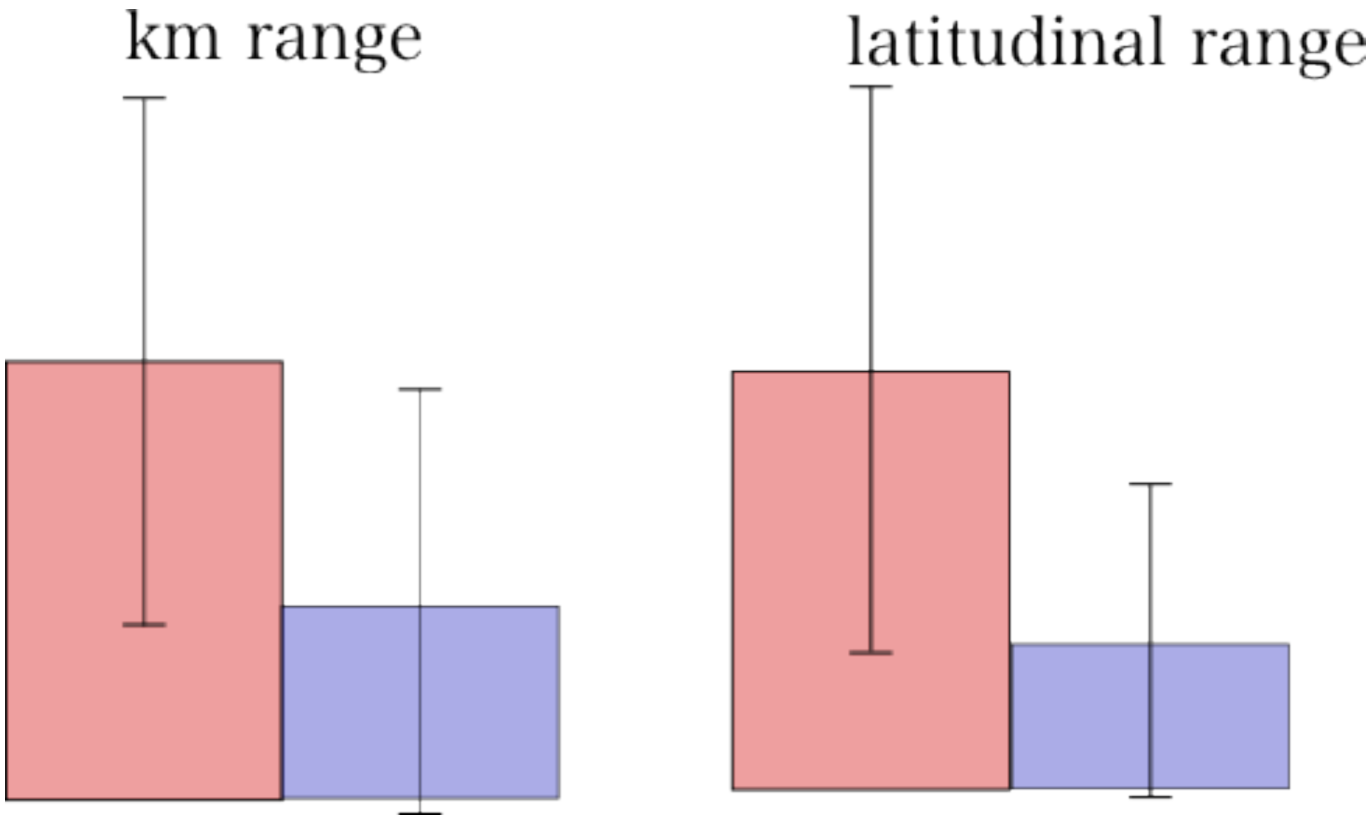
3b. Impact of specialization on speciation rate

2) MEDUSA: significant shift in speciation rate at the base of the big cosmopolitan radiation

=> possible link with generalism



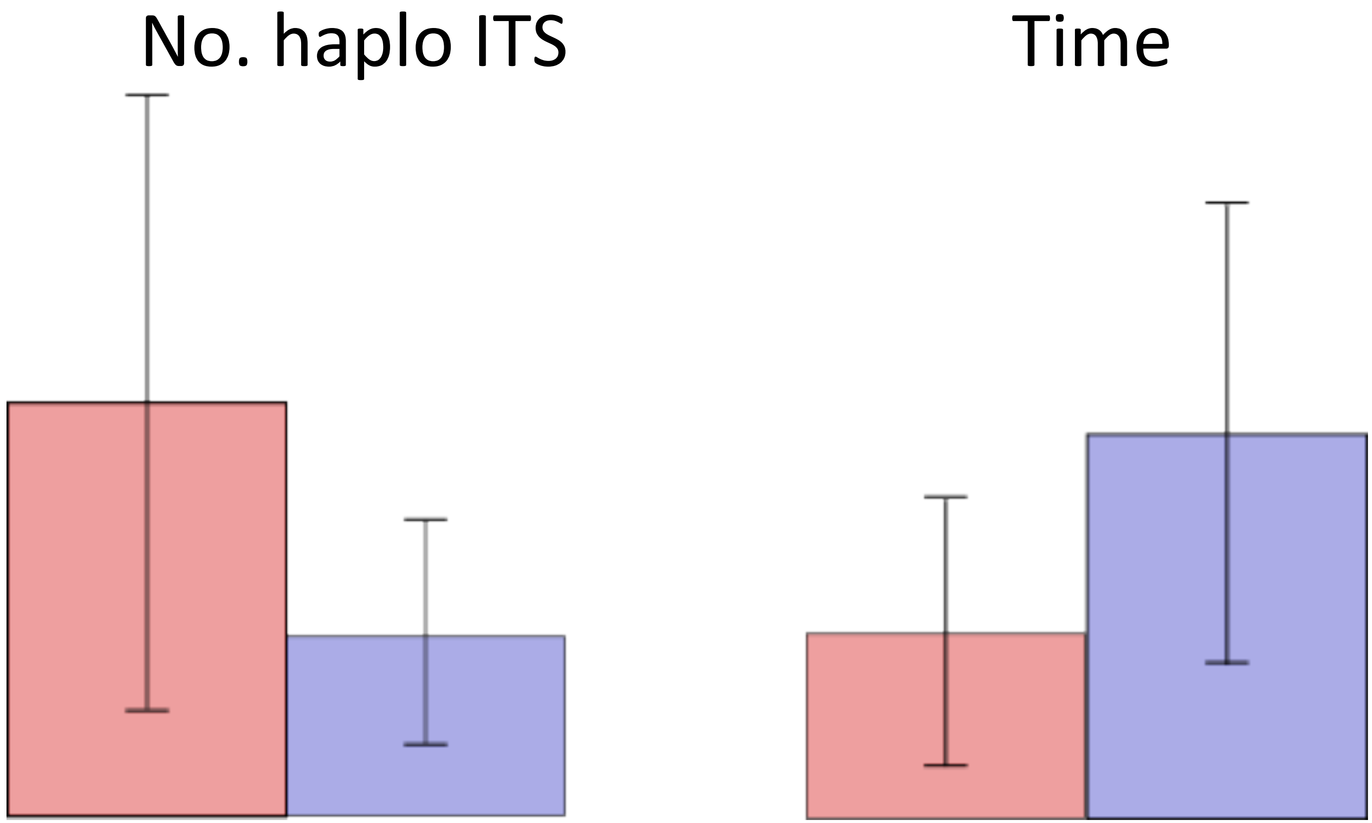
3c. Correlation between specificity and geographical range (mycobiont)



Average range of a non-specialist species: 7720 km and 27.5° of latitude

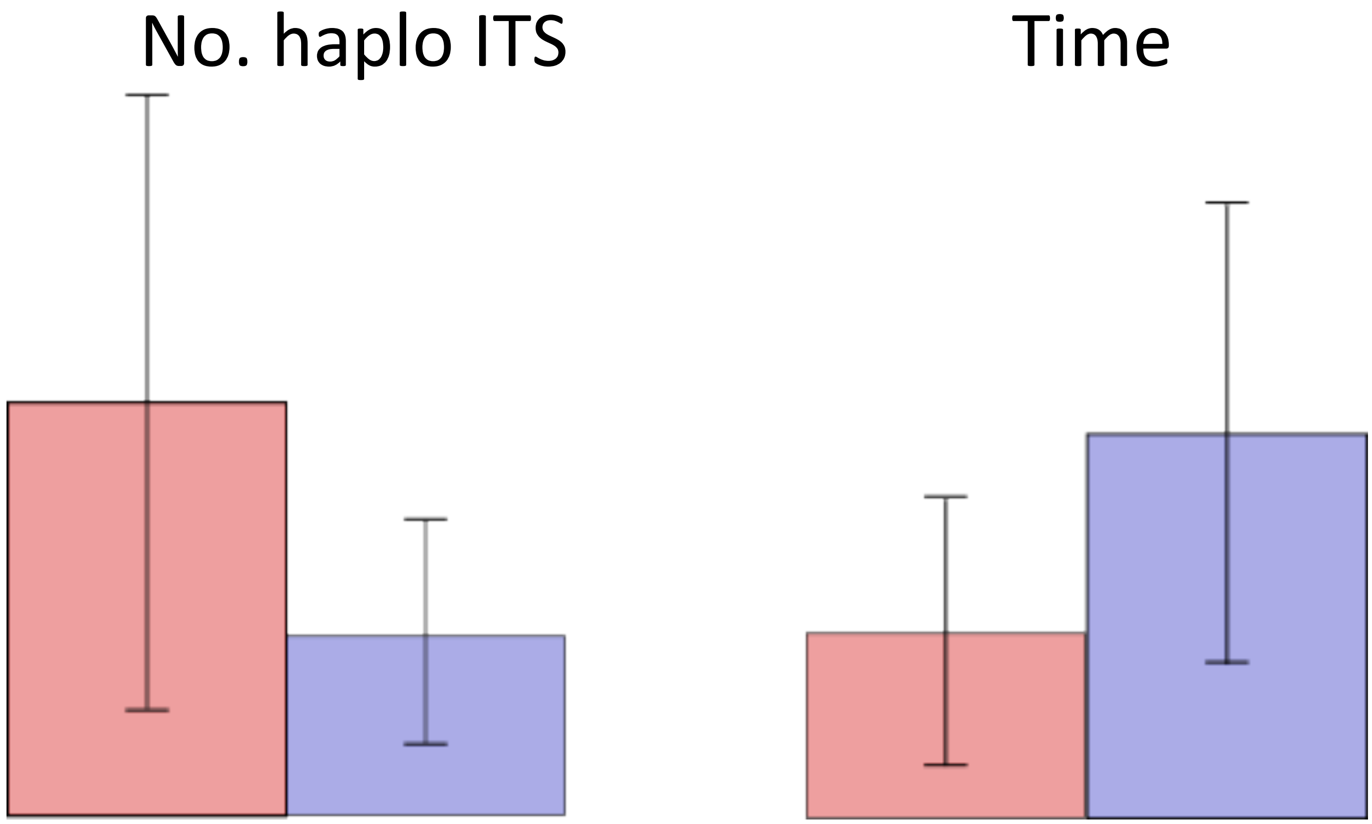
Average range of a specialist species: 3340 km and 8.5° of latitude

3d. Genetic diversity and evolution of specificity through time



- In average, less genetic variation in specialist (3.2 haplo) vs generalist (7.4) mycobiont species
- Trend of increased specialization with time (specialists on branches in average 2.1 times longer)

Law & Lewis Paradigm of mutualistic interactions



- Positive selection on the most widespread/best adapted symbiont haplotype
- Reduced diversity as a result of adaptation to a specific symbiont under specific environmental conditions

Model of evolution of lichen symbiosis

- Recent generalist species can colonize more habitats and have a wider range because they can use several symbionts present in different regions or environments.
- But through time, species can specialize on certain photobionts to optimize the fitness of the symbiosis, resulting in a narrower distribution, and reducing their genetic diversity.
- Specializing on different photobionts in different places might lead to isolation, divergence and speciation.
- Expanding to new environments might restore a more generalist selection of *Nostoc.*
- Mycobiont switching to a different *Nostoc* phylogroup might expand the geographical range of the species and eventually lead to speciation.

Thank you very much for your attention !

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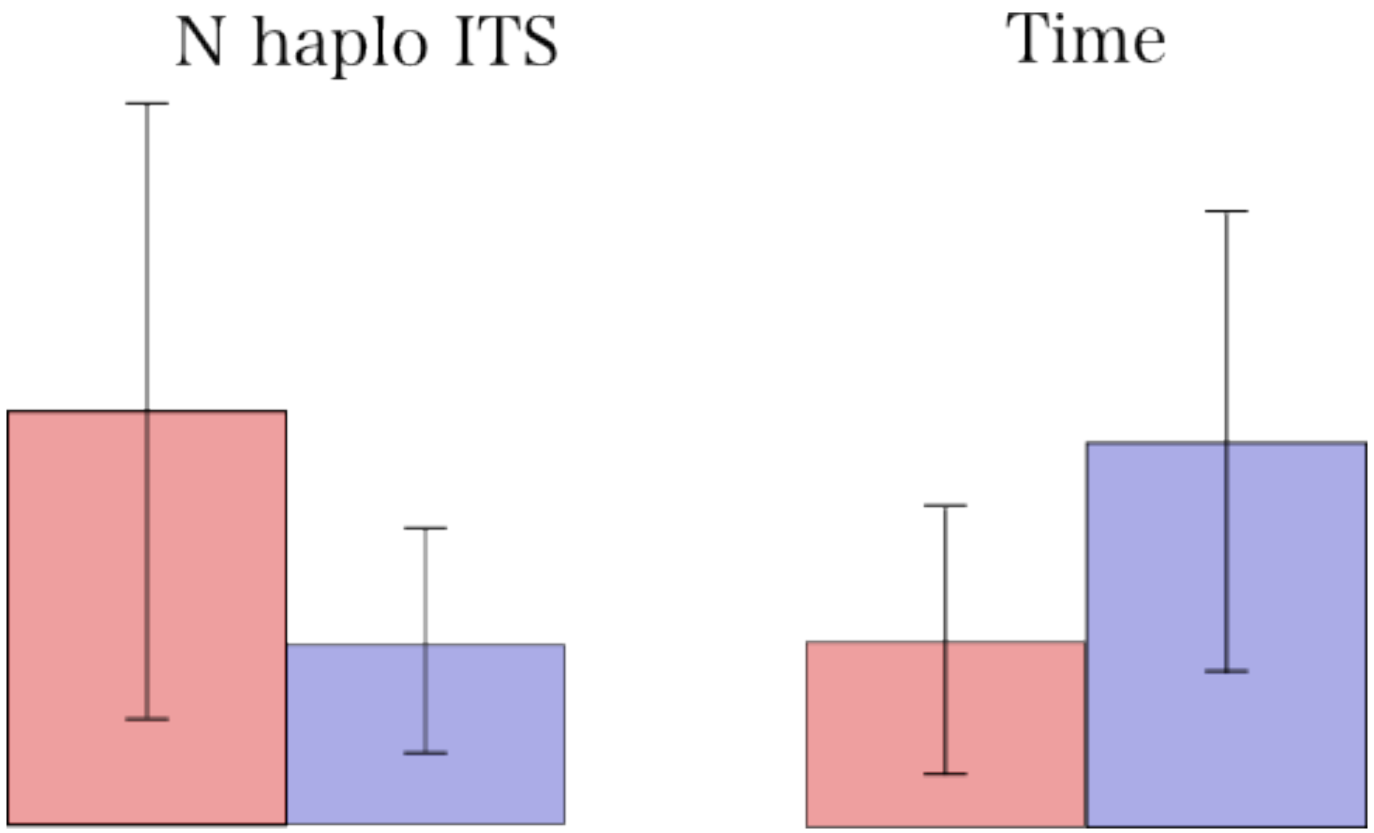
Red King Hypothesis



As the two partners need to find an equilibrium for the symbiosis, the slowest evolving partner might gain benefits by being the slowest to adapt on the way to the equilibrium and therefore the one which can stay more selfish, while the other one will have to become more generous, favoring slow evolution of the partners