Should the evolutionary lineages within *Phytophthora ramorum*, *P. lateralis* and other *Phytophthoras* be formally taxonomically designated?

Clive Brasier, Forest Research, UK
Phytophthora ramorum and P. lateralis

Phytophthora partial ITS tree

P. ramorum lineages
Ivors & Garbelotto 2004
Ivors & Garbelotto 2006
Grunwald et al 2009
Van Poucke et al 2012
*P. ramorum* / Sudden Oak death in US since ~2000 Sudden larch death in UK since ~2009

>10 million trees affected
Introduction and initial spread of four evolutionary lineages of *P. ramorum* ca 1990 - 2010

four lineages : four + introductions
“we may yet need to reconceptualise the EU and US population types as two (partially reproductively isolated ?) subspecies of *P. ramorum*: eg. subspecies *europaea* and subspecies *americana*…….”
Several media x temperature combinations gave excellent visual discrimination of the four lineages of *P. ramorum*.
P. ramorum lineages growth rates and growth optima

Franceschini et al (2013)

P. ramorum lineages sporangial dimensions

breadth

EU2
EU1 fr
EU1 o
NA2
NA1

length

2.07 x

Franceschini & Brasier
Comparative host range NA1 vs EU1

NA1

EU1

Essentially similar host ranges

Comparative aggressiveness of the lineages -

Tests on *Q. rubra*, *Q. robur* and *Fagus sylvatica* - results broadly similar

Will show *Q. rubra* results:
Aggressiveness: lesion area NA1 vs EU1

bark of *Quercus rubra* 20°C

Mean lesion area (cm²)

**EU isolates**
Mean = 36.8 ± 2.7

**US isolates**
Mean = 14.0 ± 1.8

*P. nemorosa*

Phylogenetic discrimination of lineages -
In addition to their phenotypic and phylogenetic differences

- Inter lineage sexual fecundity is low with high levels of oosphere and oospore abortion (Brasier & Kirk 2004)

- Inter lineage oospore progeny show a high frequency of non-Mendelian segregation and aberrant genome sizes – aneuploidy (Boutet et al 2010).

- Hence the genomes of the lineages appear incongruent - ie genetically diverged. Post zygotic reproductive isolation.
In which case we are probably dealing with populations which have at least partly speciated through adaptation and drift.

But we cannot be sure of the underlying evolutionary processes until we identify the original geographic origins of the lineages.

Furthermore, coalescence analysis indicates the lineages probably diverged >100K years ago from a sexually reproducing population (Goss et al. 2009).
*P. lateralis*

Introduced on *Chamaecyparis* in US Pacific Northwest

Photos Don Goheen USDA FS
2008 we discovered *P. lateralis* in old growth *Chamaecyparis obtusa* stands in Taiwan - endemic.
Identified four *P. lateralis* lineages.
Known lineage distribution 2012:

- PNW lineage
- UK lineage
- TWJ lineage
- TWK lineage

Pacific Northwest

PNW lineage

W Europe

Taiwan

TWJ lineage

TWK lineage
Phenotypes of *P. lateralis* lineages?

Brasier et al (2013)
Multivariate analysis of the four *Phytophthora lateralis* groups or lineages.

Pathogenicity:
- PNW high
- TWJ high
- UK intermediate
- TWK low

Robin et al (2014)

Brasier et al (2013)
Sequencing (five gene regions) resolves the *P. lateralis* lineages:

- Pacific Northwest
- Taiwan J
- Taiwan K
- UK

Combined nuclear tree

Brasier et al (2013)
Microsatellite analysis also resolves the *P. lateralis* lineages

**Minimum spanning network og MLGs:**

Taiwan K
Taiwan J
UK lineage

Pacific Northwest

Vettraino et al submitted
The morphological and molecular differences between the *P. ramorum* lineages - or between the *P. lateralis* lineages - appear to be as great as those between some *Phytophthora* species.

So what is the appropriate hierarchical status of these phenotypically and genetically distinct population groups or ‘lineages’?
## Lineage status - characters

<table>
<thead>
<tr>
<th>Character</th>
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| P. lateralis lineages                   | yes ✓               |               |
|                                        | no ❌                |               |
|                                        |                     |               |

- ✓: Present
- ❌: Absent
- ?: Unknown
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Review - formal and informal terms used in intraspecific classification

Fig. 25.1. Terms currently in use in intraspecific classification in relation to four dominant special interest areas.
Morphological
- Atypical form
- Morphological form
- Morphotype
- Chemotype
- Group
- Complex
- Aggregate
- Strain etc

Genetical / Physiological
- Superspecies
- Species group
- Sibling species
- Biological species
- Semi species
- Microspecies
- Mating population
- Breeding group
- Karyotype
- Genotype
- Chemotype
- Clone
- Strain etc

Hierarchical population units
- Species
- Sibling species
- Sub-species
- Race
- Genet
- Ramet

Ecological
- Population
- Sub population
- Ecotype
- Race
- Geographic race
- Local race
- Clone
- Strain
- Individual
- Isolate etc

Plant pathological
- Biological species
- Special form
- Race
- Physiologic race
- Environmental race
- Biotype
- Pathotype
- Strain etc

Phylospecies
- Clade
- Subclade
- Lineage

Brasier & Rayner 1986
Summary and conclusions

- The ‘lineages’ of *P. ramorum* (*P. lateralis*) show considerable adaptive differences and evidence of reproductive isolation.

- The phenotypic differences between the lineages are as great as those between some *Phytophthora* species.

- ‘Lineage’ is one of many informal terms. It has no formal taxonomic meaning.

  It does not convey the biological status of these populations i.e. subspecies / sibling species.
[Conclusions]

My suggestion is that the *P. ramorum* lineages should probably be formally taxonomically described at least as subspecies -

- for the purposes of accurate scientific communication, especially within the mycological community.

- to enhance understanding among plant health regulators and promote tighter biosecurity protocol.

EU1, EU2 examples...

Thank you!