A key to sustainable management of the grapevine downy mildew pathogen

François Delmotte

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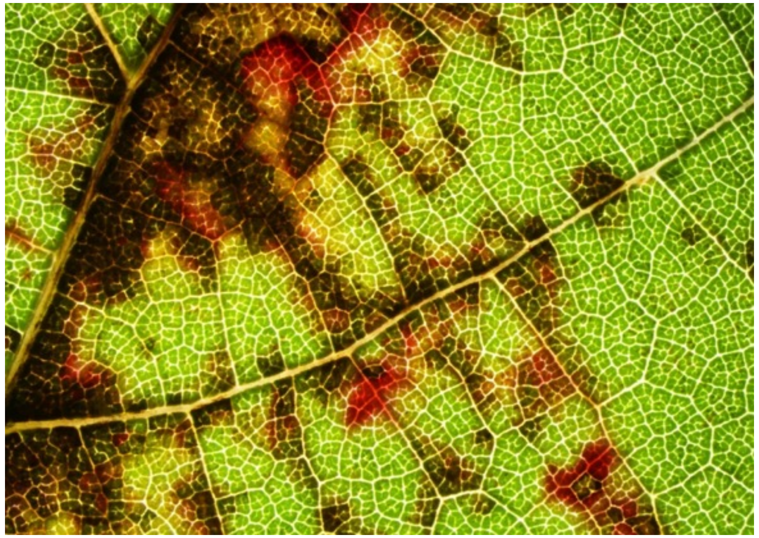
17th Congress of the Mediterranean Phytopathological Union, 6-10 July 2025, Bari, Italy

Plasmopara viticola, the grapevine downy mildew pathogen

- Major grapevine disease
- Oomycetes, biotrophic, diploid
- Mixed reproduction system, heterothallic
- Originating from north-eastern America

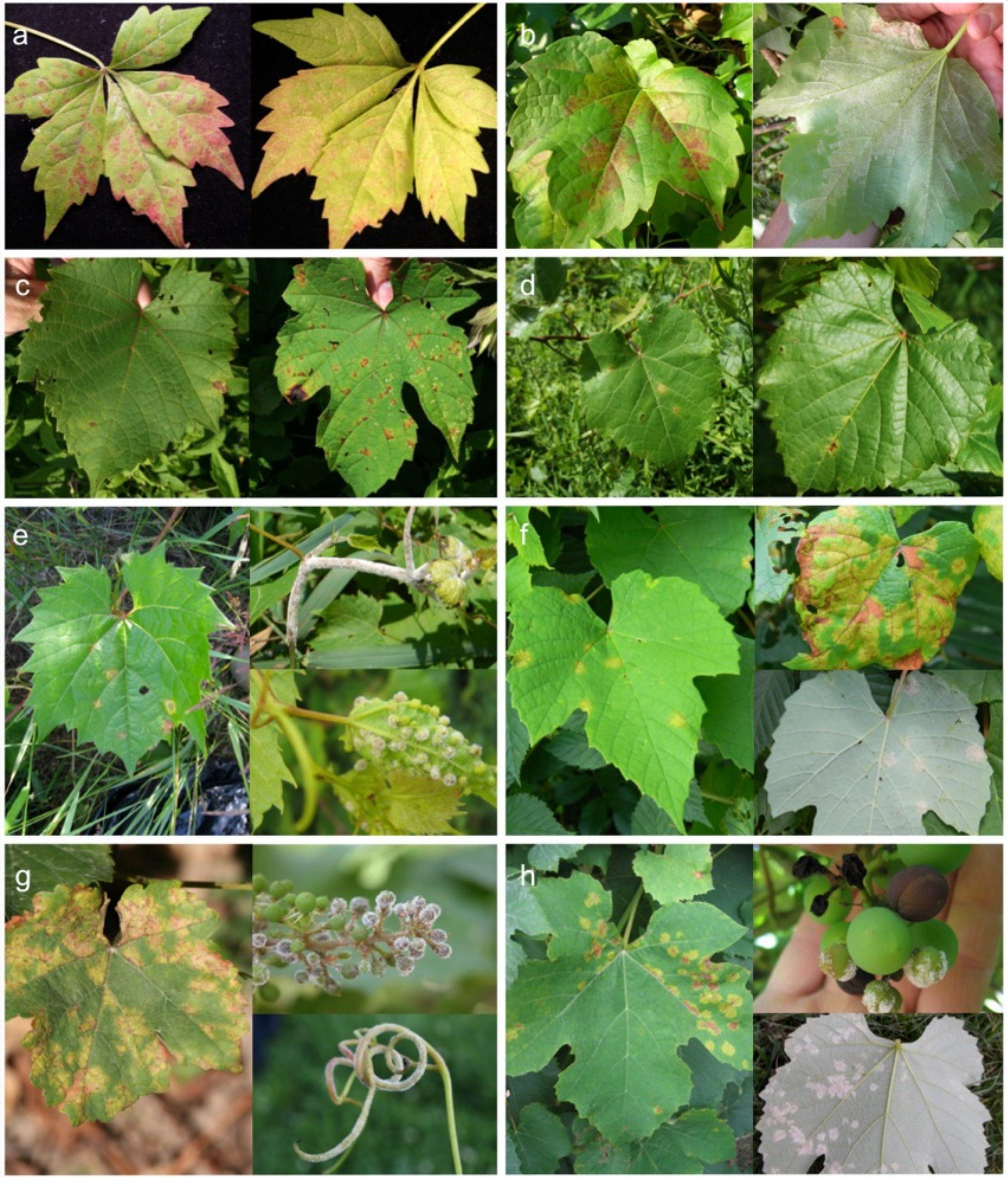


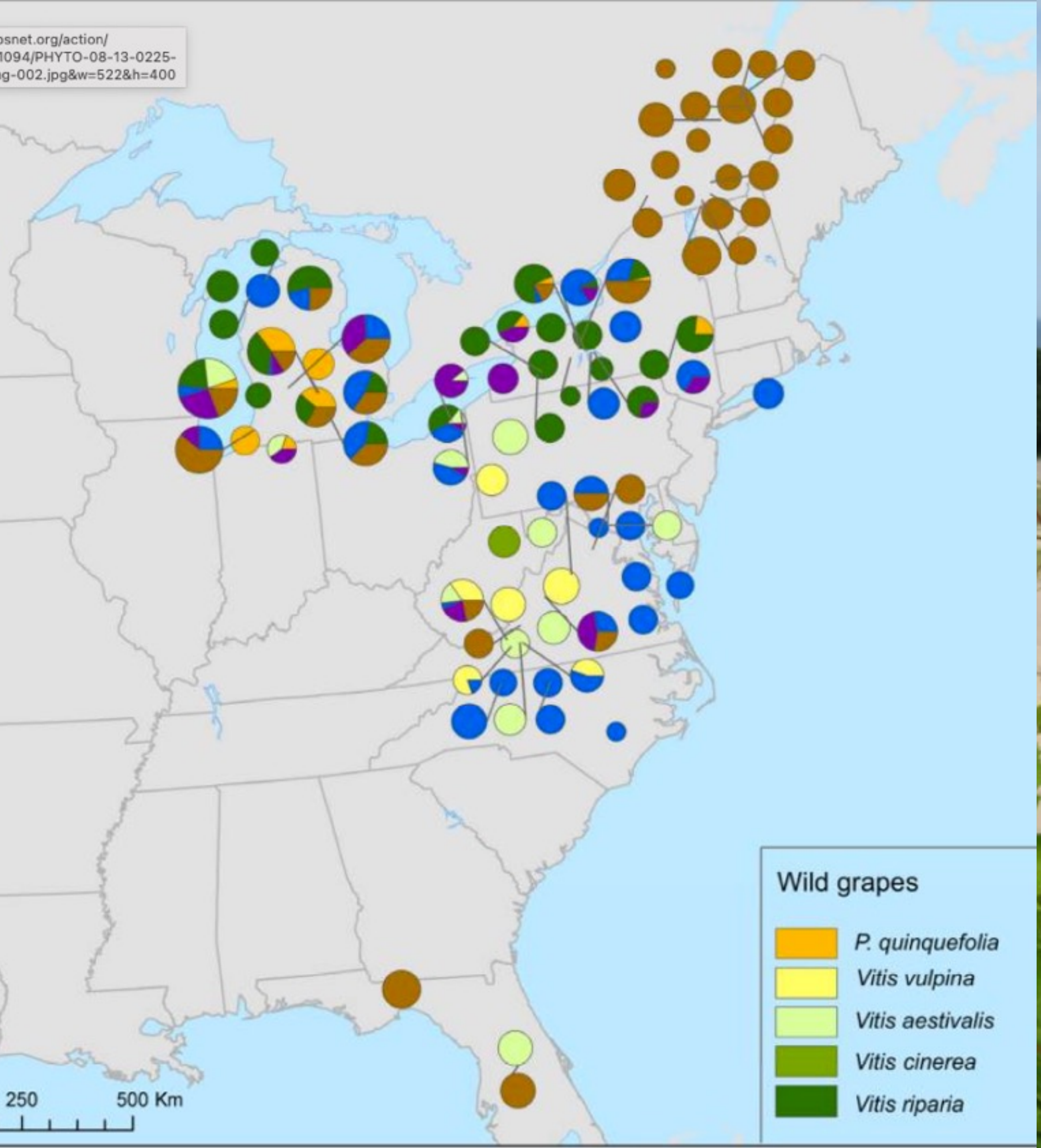
Wild american Vitis

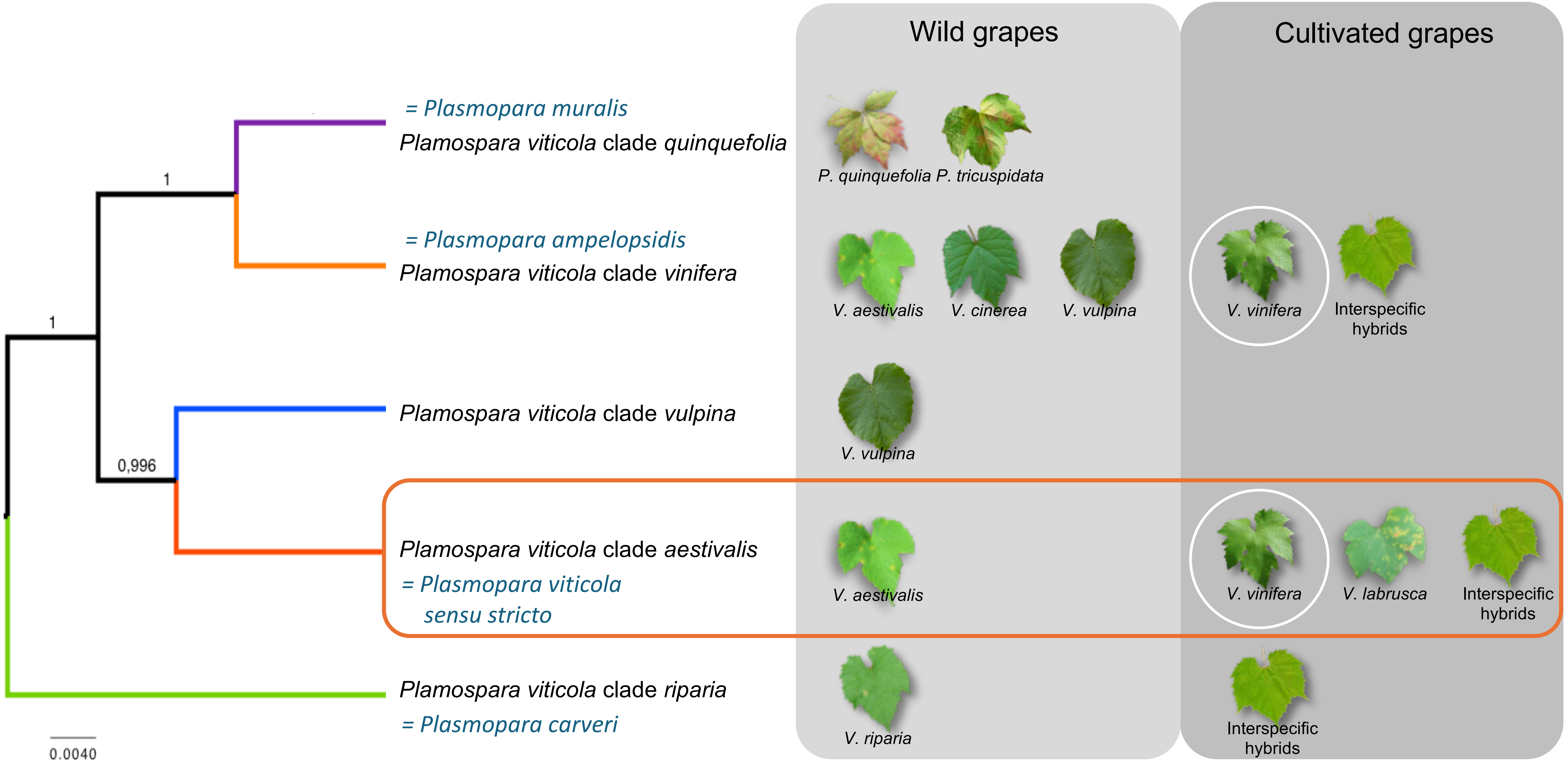
a. *Parthenocissus quinquefolia*
b. *Parthenocissus tricuspidata*
c. *V. cinerea*
d. *V. vulpina*
e. *V. riparia*
f. *V. aestivalis*

Cultivated Vitis

g. *V. vinifera*
h. *V. labruscana* (concord, niagara)




psnet.org/action/
1094/PHYTO-08-13-0225-
g-002.jpg&w=522&h=400
Wild grapes
P. quinquefolia
Vitis vulpina
Vitis aestivalis
Vitis cinerea
Vitis riparia
250
500 Km



Rouxel et al. 2013, New Phytol, 10.1111/nph.12016
Rouxel et al. 2014, Phyopathology, doi.org/10.1094/PHYTO-08-13-0225-R => P. viticola clades
Salgado-Salazar C, Thines M. Mycological Progress. 2022 Jul;21(7):63. => new Plasmopara species names (blue)

Fontaine et al. 2021, Current Biology

Please cite this article in press as: Fontaine et al., Europe as a bridgehead in the worldwide invasion history of grapevine downy mildew, *Plasmopara viticola*, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.03.009

Current Biology

CellPress

Article

Europe as a bridgehead in the worldwide invasion history of grapevine downy mildew, *Plasmopara viticola*

Michael C. Fontaine,[1,2,3,5,8,10,11,*] Frédéric Labbé,[1,2,5,6] Yann Dussert,[4,7] Laurent Delière,[4] Sylvie Richart-Cervera,[4] Tatiana Giraud,[2] and François Delmotte[4,9,*]

[1]Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, P.O. Box 11103 CC, Groningen, the Netherlands
[2]Ecologie Systématique et Evolution, UMR 8079, Université Paris-Saclay, CNRS, AgroParisTech, Orsay 91400, France
[3]Laboratoire MIVEGEC (Université de Montpellier, CNRS 5290, IRD 229) et Centre de Recherche en Écologie et Évolution de la Santé (CREES), Institut de Recherche pour le Développement (IRD), 34394 Montpellier, France
[4]SAVE, INRAE, Bordeaux Sciences Agro, Université de Bordeaux, 33140 Villenave d'Ornon, France
[5]These authors contributed equally
[6]Present address: Department of Ecology and Evolution, University of Chicago, Chicago, IL, USA
[7]Present address: School of Biological and Chemical Sciences, Queen Mary University of London, London, UK
[8]Twitter: @MikaFontaine1
[9]Twitter: @PacoDelmotte
[10]Twitter: @GenEcoEvo
[11]Lead contact
*Correspondence: michael.fontaine@cnrs.fr (M.C.F.), francois.delmotte@inrae.fr (F.D.)
https://doi.org/10.1016/j.cub.2021.03.009

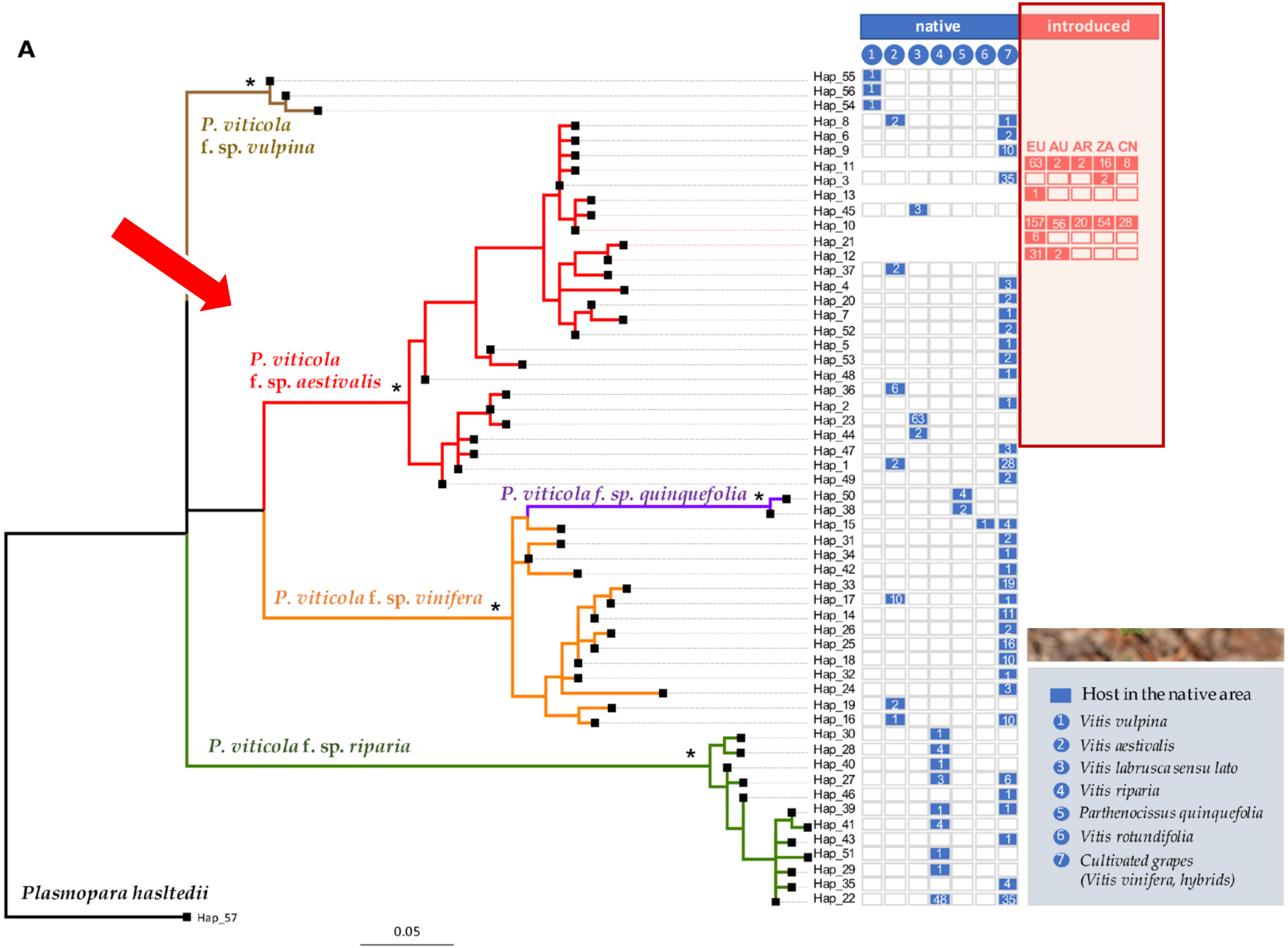
SUMMARY

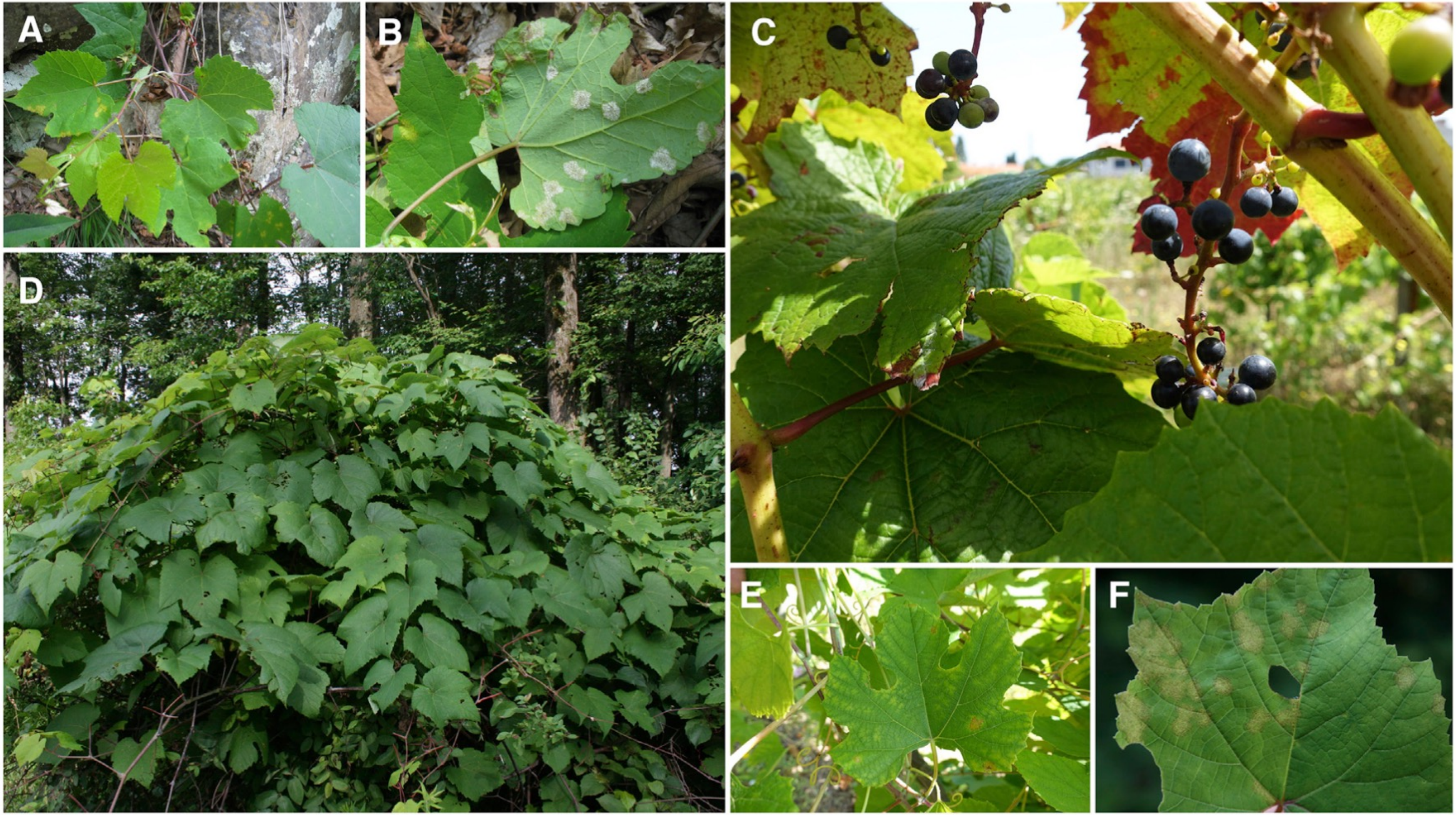
Europe is the historical cradle of viticulture, but grapevines (*Vitis vinifera*) have been increasingly threatened by pathogens of American origin. The invasive oomycete *Plasmopara viticola* causes downy mildew, one of the most devastating grapevine diseases worldwide. Despite major economic consequences, its invasion history remains poorly understood. We analyzed a comprehensive dataset of ∼2,000 samples, collected from the most important wine-producing countries, using nuclear and mitochondrial gene sequences and microsatellite markers. Population genetic analyses revealed very low genetic diversity in invasive downy mildew populations worldwide and little evidence of admixture. All the invasive populations originated from only one of the five native North American lineages, the one parasitizing wild summer grape (*V. aestivalis*). An approximate Bayesian computation-random forest approach allowed inferring the worldwide invasion scenario of *P. viticola*. After an initial introduction into Europe, invasive European populations served as a secondary source of introduction into vineyards worldwide, including China, South Africa, and twice independently, Australia. Only the invasion of Argentina probably represents a tertiary introduction, from Australia. Our findings provide a striking example of a global pathogen invasion resulting from secondary dispersal of a successful invasive population. Our study will also help designing quarantine regulations and efficient breeding for resistance against grapevine downy mildew.

INTRODUCTION

Global changes (e.g., climate warming and international exchanges) are favoring increases in the numbers of emerging diseases caused by invasive pathogens on crops worldwide, incurring substantial economic, social, and environmental costs.[1–4] Infamous recent examples include the emergence of new races of the stem rust fungus in Eastern Africa[5] and Europe[6,7] and of the fungus causing wheat blast disease in Bangladesh,[8] both threatening wheat production and becoming invasive. Most emerging diseases result from biological invasions bringing the native host-parasite association back together after crop introduction into new areas, or host shifts following pathogen introductions.[9,10] An understanding of the evolutionary processes responsible for emerging crop diseases is important for preventing further devastating biological invasions and for controlling introduced populations. This requires elucidation of the invasion mechanisms, pathways, and demographic processes occurring during pathogen invasions (e.g., bottlenecks and hybridization). Important questions include whether pathogen invasions result from host shifts, whether limited genetic variation has been introduced, whether multiple introductions and admixture are required for successful invasions,[10] and whether the invaded areas are colonized directly from native populations or whether an initial successful invasive population serves as the source for secondary introductions.

Grapevine (*Vitis vinifera* subsp. *sativa* L.) is one striking case of crop threatened by invasive pests. This emblematic crop has a prominent place in the history of European civilization. Grapevine domestication started 8,000 years ago from

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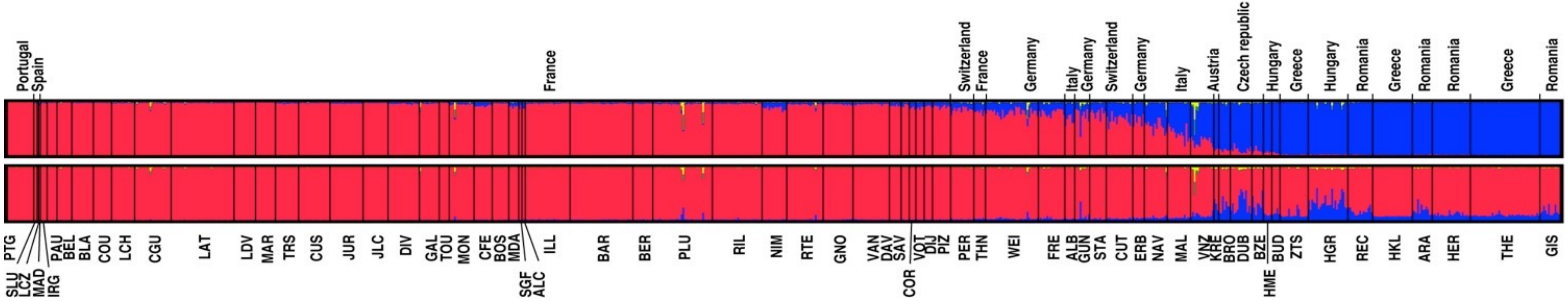


Fontaine et al. 2013, Mol Ecol

MOLECULAR ECOLOGY

Molecular Ecology (2013) doi: 10.1111/mec.12293

Genetic signature of a range expansion and leap-frog event after the recent invasion of Europe by the grapevine downy mildew pathogen *Plasmopara viticola*

MICHAEL C. FONTAINE,*† FRÉDERIC AUSTERLITZ,*† TATIANA GIRAUD,* FRÉDÉRIC LABBÉ,* DACIANA PAPURA,‡ SYLVIE RICHARD-CERVERA‡ and FRANÇOIS DELMOTTE‡

**Ecologie, Systématique et Evolution, UMR 8079 Université Paris Sud Laboratoire Ecologie, Systematique et Evolution, UMR8079, Orsay Cedex, F-91405, France, †Eco-Anthropologie et Ethnobiologie, UMR 7206 CNRS, MNHN, Univ Paris Diderot, Sorbonne Paris Cité, F-75231 Paris Cedex 5, France, ‡INRA, UMR1065 Santé et Agroécologie du Vignoble, ISVV, F-33883 Villenave d'Ornon Cedex, France*

Abstract

Biologic invasions can have important ecological, economic and social consequences, particularly when they involve the introduction and spread of plant invasive pathogens, as they can threaten natural ecosystems and jeopardize the production of human food. Examples include the grapevine downy mildew, caused by the oomycete *Plasmopara viticola*, an invasive species native to North America, introduced into Europe in the 1870s. We investigated the introduction and spread of this invasive pathogen, by analysing its genetic structure and diversity in a large sample from European vineyards. Populations of *P. viticola* across Europe displayed little genetic diversity, consistent with the occurrence of a bottleneck at the time of introduction. Bayesian coalescent analyses revealed a clear population expansion signal in the genetic data. We detected a weak, but significant, continental-wide population structure, with two geographically and genetically distinct clusters in Western and Eastern European vineyards. Approximate Bayesian computation, analyses of clines of genetic diversity and of isolation-by-distance patterns provided evidence for a wave of colonization moving in an easterly direction across Europe. This is consistent with historical reports, first mentioning the introduction of the disease in Bordeaux vineyards (France) and subsequently documenting its rapid spread across Europe. This initial introduction in the west was probably followed by a 'leap-frog' event into Eastern Europe, leading to the formation of the two genetic clusters we detected. This study shows that recent population genetics methods within the Bayesian and coalescence frameworks are extremely powerful for increasing our understanding of pathogen population dynamics and invasion histories.

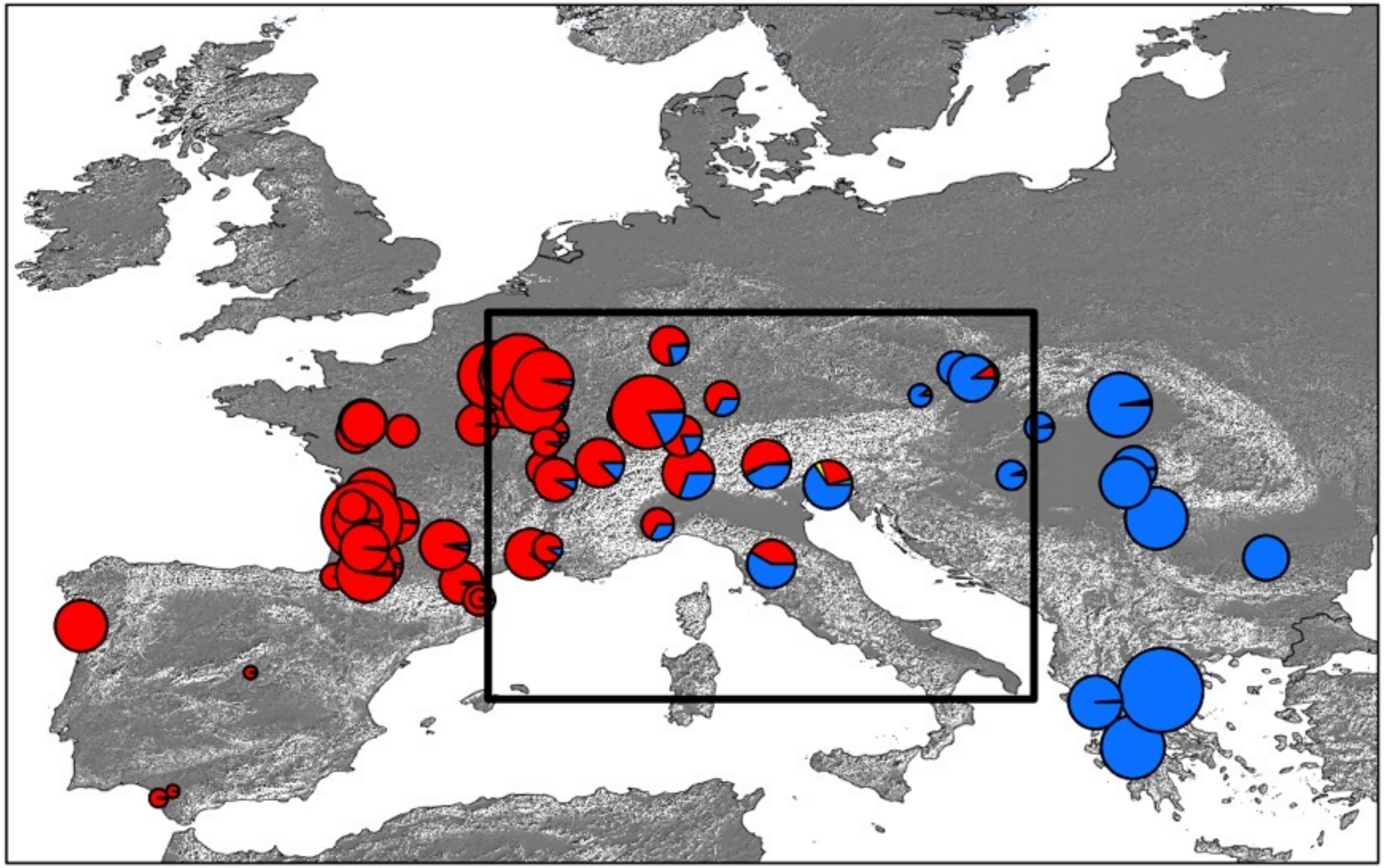
Keywords: fungi, invasive plant pathogen, microsatellite, oomycetes, population genetics, recent introduction, *Vitis vinifera*

Received 16 November 2012; revision received 11 February 2013; accepted 14 February 2013

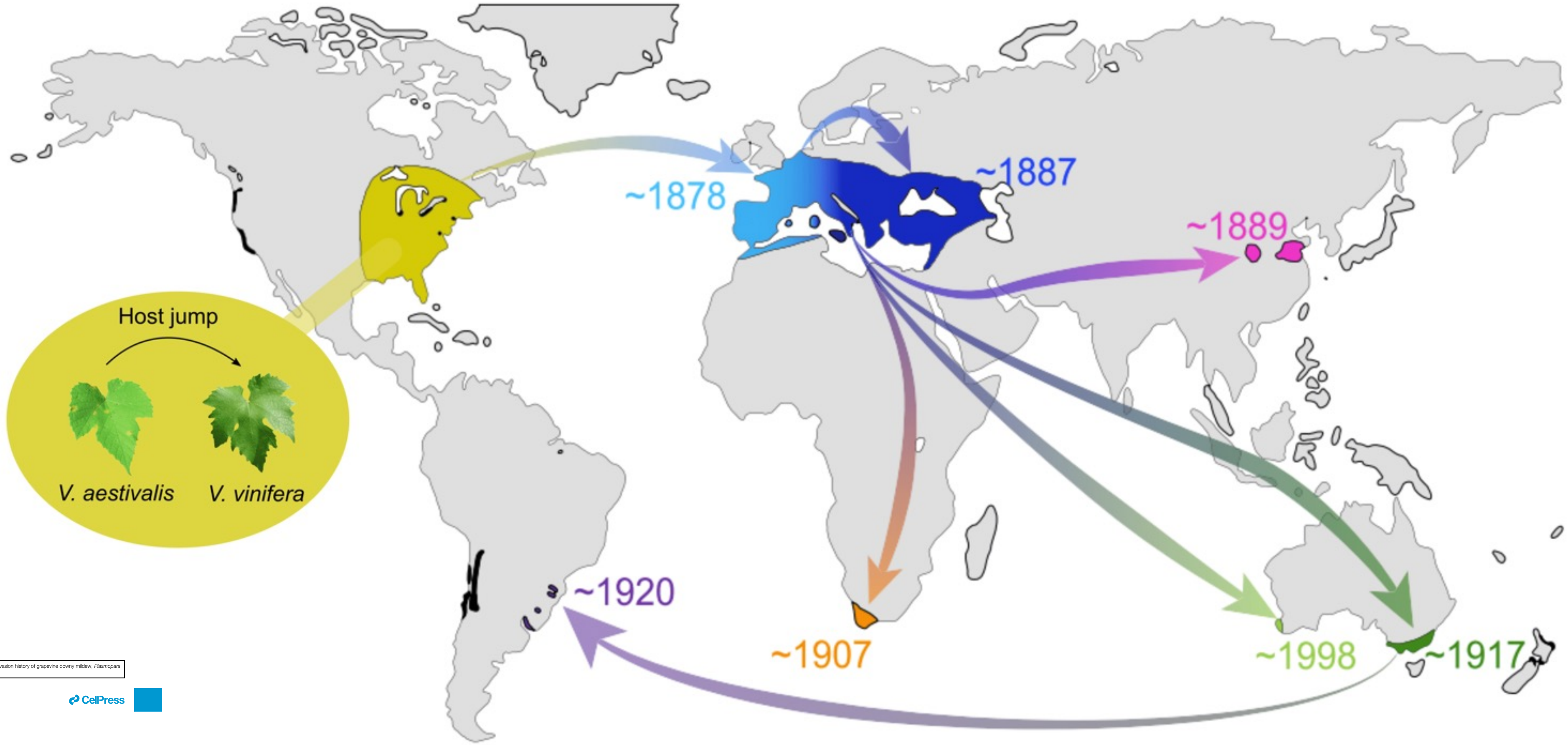
Introduction

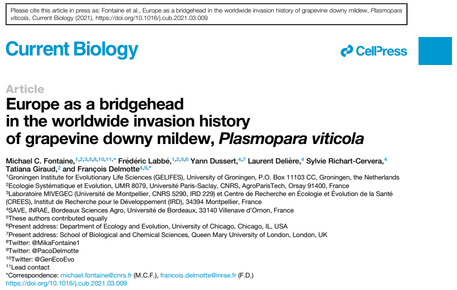
Biologic invasions can have important ecological, economic and social consequences (Pimentel *et al*. 2001), particularly when they involve the introduction and spread of pathogens (Anderson *et al*. 2004). Considerable attention is focused on human and animal diseases, but outbreaks of disease due to invasive pathogens are also becoming increasingly frequent in plants (Desprez-Loustau *et al*. 2007). Plant diseases can threaten natural ecosystems and jeopardize the production of human food (Giraud *et al*. 2010). Many pathogens of agricultural systems are believed to be alien in the areas in which they cause damaging epidemics (Pimentel *et al*. 2001). With the same crops being cultivated worldwide and the

Correspondence: Michael C. Fontaine, Fax: +1-574-631-3996; E-mail: mikafontaine@gmail.com



Worldwide invasion of *P. viticola* from North America





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Current Biology
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Europe as a bridgehead in the worldwide invasion history of grapevine downy mildew, *Plasmopara viticola*

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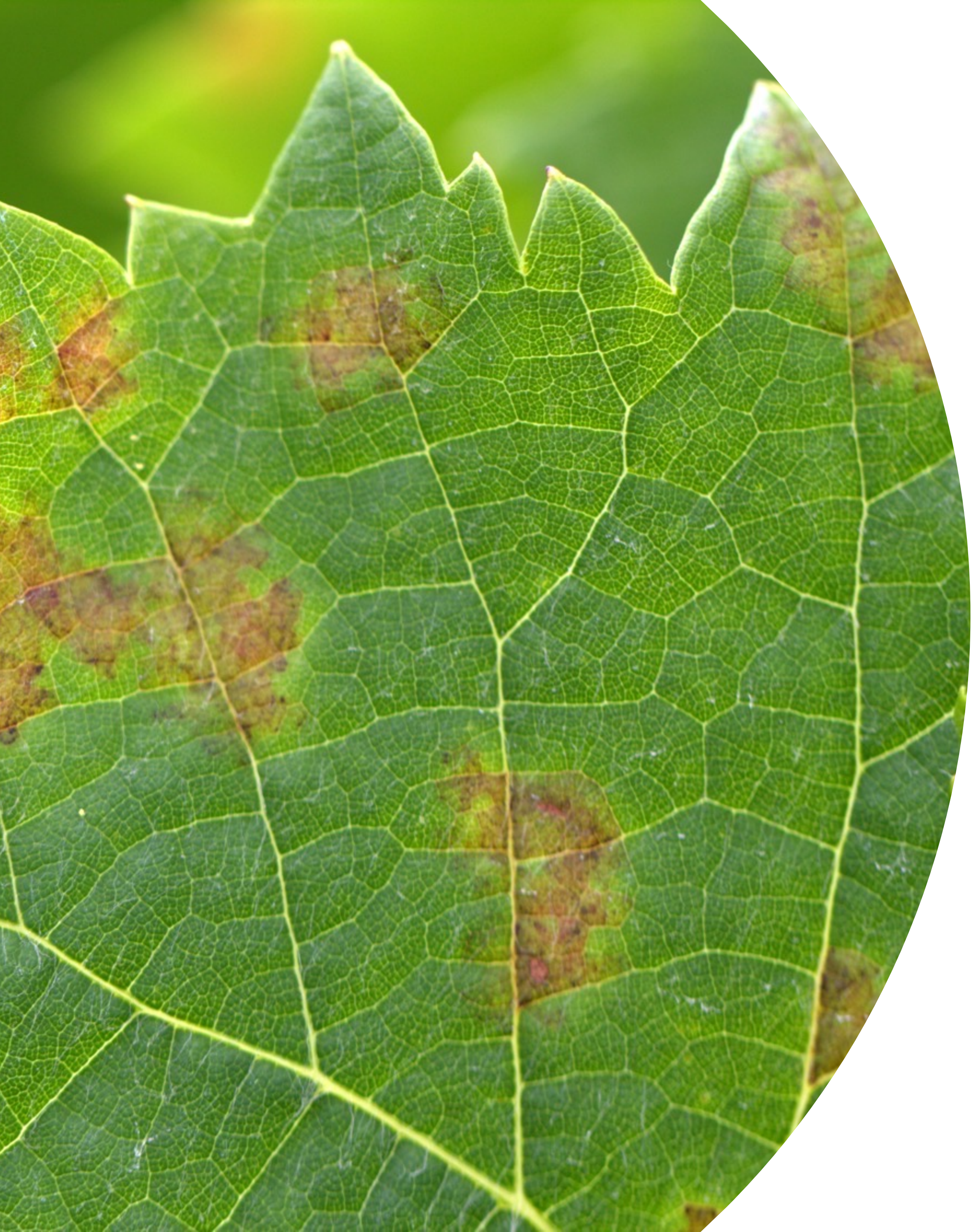
[4]SAVE, INRAE, Bordeaux Sciences Agro, Université de Bordeaux, 33140 Villenave d'Ornon, France
[5]These authors contributed equally
[6]Present address: Department of Ecology and Evolution, University of Chicago, Chicago, IL, USA
[7]Present address: School of Biological and Chemical Sciences, Queen Mary University of London, London, UK
[8]Twitter: @MikaFontaine1
[9]Twitter: @PacoDelmotte
[10]Twitter: @GenEcoEvo
[11]Lead contact
*Correspondence: michael.fontaine@cnrs.fr (M.C.F.), francois.delmotte@inrae.fr (F.D.)
https://doi.org/10.1016/j.cub.2021.03.009

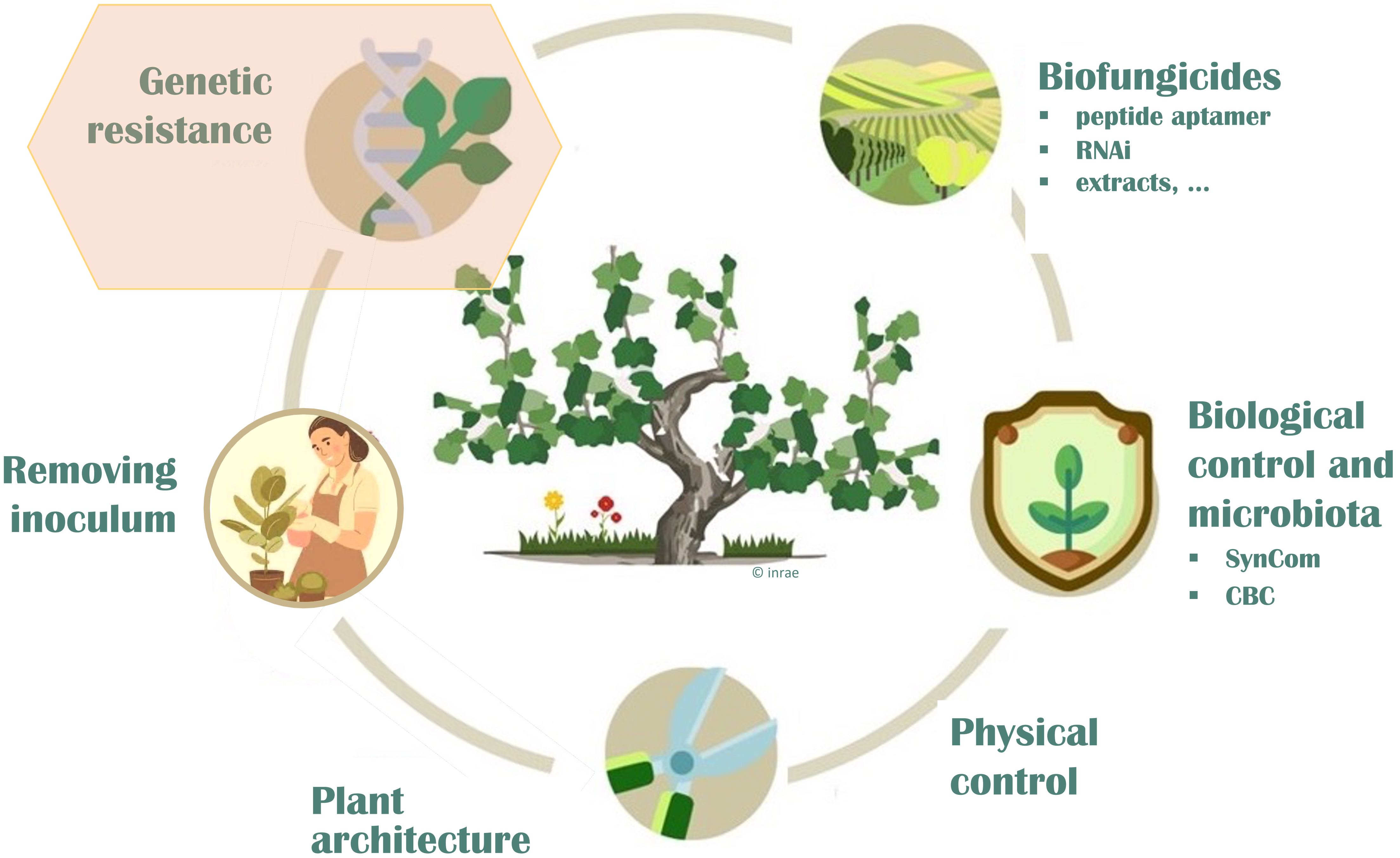
Fontaine et al., 2021, Current Biol.



- Cultivated varieties are all **highly susceptible**
- Strong impact on **harvest quantity and quality**
- Polycyclic development leading to **numerous preventive treatments**

- Withdrawal of fungicide molecules
- CC - increased unpredictability of conducive climatic conditions
- Rapid evolution

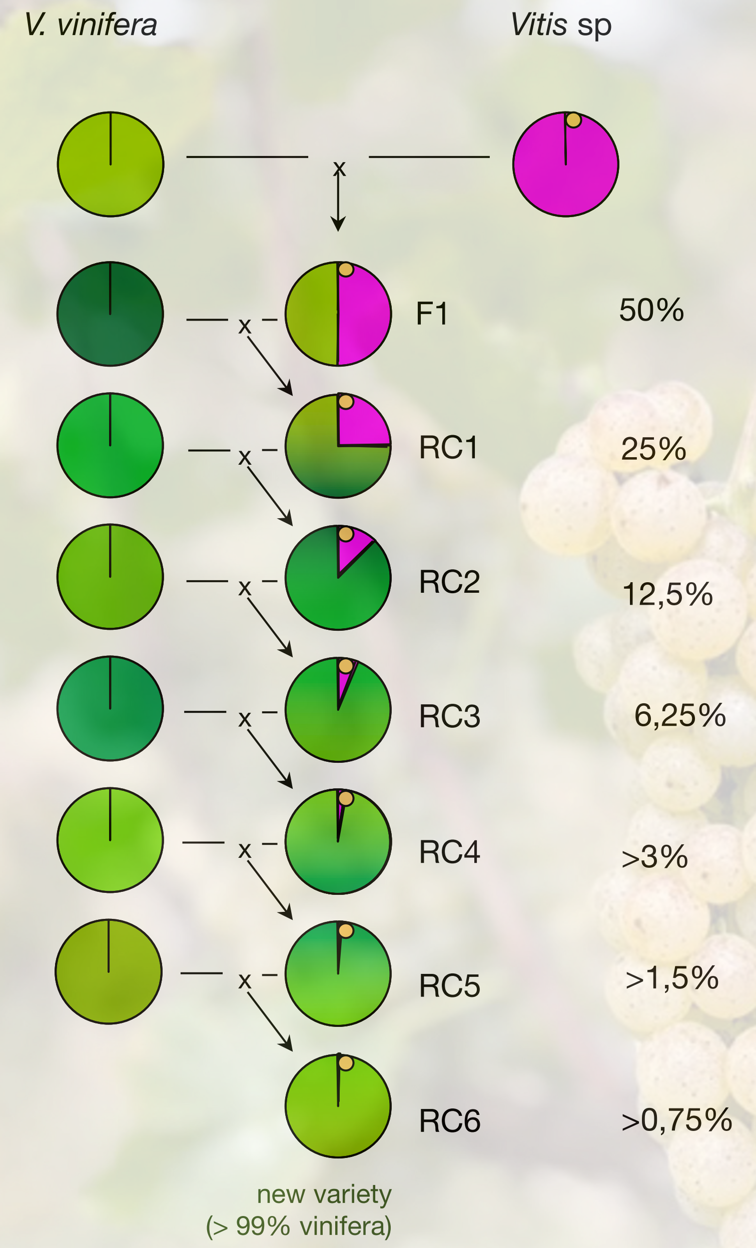
Research to renew our knowledge to find sustainable management methods **alternative to fungicides**


Genetic resistance
Biofungicides
peptide aptamer
RNAi
extracts, ...
Biological control and microbiota
SynCom
CBC
Removing inoculum
© inrae
Physical control
Plant architecture

Conventional breeding programs have created a new generation of disease-resistant varieties with excellent agronomic and organoleptic characteristics.

- 14 INRAE resistant varieties « classée » [total=30]
- 3 000 ha planted in France
- 1400 ha of INRAE var. res.
- -80% of treat. freq. index

The challenges for the future are
- wine quality
- adaptation to CC
- **durability of resistance**



P. viticola is quicky adapting to resistant varieties

Peressotti *et al. BMC Plant Biology* 2010, **10**:147
http://www.biomedcentral.com/1471-2229/10/147

BMC Plant Biology

RESEARCH ARTICLE Open Access

Breakdown of resistance to grapevine downy mildew upon limited deployment of a resistant variety

Elisa Peressotti[1,4], Sabine Wiedemann-Merdinoglu[1,2], François Delmotte[3], Diana Bellin[4,6], Gabriele Di Gaspero[4,5], Raffaele Testolin[4,5], Didier Merdinoglu[1,2], Pere Mestre[1,2*]

Abstract

Background: Natural disease resistance is a cost-effective and environmentally friendly way of con
disease. Breeding programmes need to make sure that the resistance deployed is effective and du
downy mildew, caused by the Oomycete *Plasmopara viticola*, affects viticulture and it is controlled
Downy mildew resistant grapevine varieties are a promising strategy to control the disease, but th
currently restricted to very limited acreages. The arising of resistance-breaking isolates under such
deployment of resistant varieties would provide valuable information to design breeding strategies
deployment of resistance genes over large acreages whilst reducing the risks of the resistance bei
observation of heavy downy mildew symptoms on a plant of the resistant variety Bianca, whose re
conferred by a major gene, provided us with a putative example of emergence of a resistance-bre
the interaction between grapevine and *P. viticola*.

Results: In this paper we describe the emergence of a *P. viticola* isolate (isolate SL) that specifically
Rpv3, the major resistance gene carried by Bianca at chromosome 18. We show that isolate SL has
behaviour as two *P. viticola* isolates avirulent on Bianca (isolates SC and SU) when inoculated on su
or on resistant plants carrying resistances derived from other sources, suggesting there is no fitnes
to the virulence. Molecular analysis shows that all three isolates are genetically closely related.

Conclusions: Our results are the first description of a resistance-breaking isolate in the grapevine/
interaction, and show that, despite the reduced genetic variability of *P. viticola* in Europe compare
origin and the restricted use of natural resistance in European viticulture, resistance-breaking isolate
monogenic resistances may arise even in cases where deployment of the resistant varieties is limit
acreages. Our findings represent a warning call for the use of resistant varieties and an incentive t
breeding programmes aiming to optimize durability of the resistances.

Background

Natural disease resistance is a cost-effective and environment friendly way of controlling plant disease. Breeding programmes aiming to obtain disease resistant varieties have been developed for most plants of economical interest. An important challenge of breeding for disease resistance is durability. Plant disease resistance is defined as durable when it "remains effective during its prolonged and widespread use in an environment favourable to disease" [1]. The extent t durable resistance is difficult is highli that most varieties deployed possessing monogenic resistance had been rapidly overcome because of changes in pathogen populations [2,3] (and references therein). As an illustration, [4] lists over 267 resistance genes from 14 pathosystems that proved not to be durable when used as single genes. The durability of the resistance may be improved, among other strategies, by the use of varietal mixtures [5-7] or by pyramiding genes [3]. In any case, a sound knowledge of the biological and genetic components of the pathosystem is important to

* Correspondence: pere.mestre@colmar.inra.fr
[1]INRA, UMR1131 Santé de la Vigne et Qualité du Vin, F-68000 Colmar, France

Evolutionary Applications Open Access
Evolutionary Applications ISSN 1752-4571

ORIGINAL ARTICLE

Adaptation of a plant pathogen to partial host resistance:

Grapevine resistances loci have been largely described while the specific efectors detected by grape resistance genes and evolutionary mechanisms leading to resistance breakdowns in *P. viticola* remain entirely unknown.

of their deployment on fungicide use in viticulture

Chantal Wingerter[1,2†], Birgit Eisenmann[1†], Patricia Weber[2], Ian Dry[3] and Jochen Bogs[1,4*]

Abstract

Background: The high susceptibility of European grapevine cultivars (*Vitis vinifera*) to downy mildew (*Plasmopara viticola*) leads to the intensive use of fungicides in viticulture. To reduce this input, breeding programs have introgressed resistance loci from wild *Vitis* species into *V. vinifera*, resulting in new fungus-resistant grapevine cultivars (FRC). However, little is known about how these different resistance loci confer resistance and what the potential reduction in fungicide applications are likely to be if these FRCs are deployed. To ensure a durable and sustainable resistance management and breeding, detailed knowledge about the different defense mechanisms mediated by the respective *Rpv* (*Resistance to P. viticola*) resistance loci is essential.

Results: A comparison of the resistance mechanisms mediated by the *Rpv3–1*, *Rpv10* and/or *Rpv12*-loci revealed an early onset of programmed cell death (PCD) at 8 hours post infection (hpi) in *Rpv12*-cultivars and 12 hpi in *Rpv10*-cultivars, whereas cell death was delayed in *Rpv3*-cultivars and was not observed until 28 hpi. These temporal differences correlated with an increase in the *trans*-resveratrol level and the formation of hydrogen peroxide shortly before onset

Phytopathology®

The characterization of pathotypes in grapevine downy mildew provides insights into the breakdown of Rpv3, Rpv10 and Rpv12 factors in grapevines

Paineau[a], Isabelle D. Mazet[a], Sabine Wiedemann-Merdinoglu[b], Frédéric Fabre[a,1], and François Delmotte[a,1]
[a]INRAE, Bordeaux Sciences Agro, SAVE, ISVV, Villenave d'Ornon, F-33140, France
[b]INRAE, Université de Strasbourg, SVQV, Colmar, F-68000, France
[1]These authors contributed equally to the article.

standard method for characterizing the virulence *smopara viticola*, the causal agent of grapevine w. We used 33 European strains to inoculate six ieties carrying the principal factors for resistance dew (Rpv1; Rpv3.1; Rpv3.2; Rpv5, Rpv6; Rpv10 nd the susceptible *Vitis vinifera* cv. Chardonnay. raction, we characterized the level of sporulation lysis and the intensity of the grapevine hypersen- e by visual score. We propose a definition for n of grapevine quantitative resistances combining its. Among the 33 strains analyzed, 28 are viru- st one resistance factor. We identified five differ- s across the 33 strains analyzed: two pathotypes single resistance factor (vir3.1 and vir3.2) and x pathotypes overcoming multiple resistance fac- 2; vir3.2,12; vir3.1,3.2,10). Our findings confirm d occurrence of *P. viticola* strains overcoming the pes (28 strains). We also detected the first break- tance to the Rpv10 by a strain from Germany and n of Rpv12 factors by a strain in Hungary. The method proposed here and the associated differen- lay the groundwork for the early detection of resistance breakdown in grapevines. This approach will also facilitate the monitoring of the evolution of *P. viticola* populations at large spatial scales. This is an essential step forward to promoting durable management of the resistant grapevine varieties currently available.

Pathotype, Plant-pathogen interaction, *Plasmopara viticola*, Quantitative resistance, Resistance breakdown, Resistance durability
Correspondence: *frederic.fabre@inrae.fr*

Associated publication

Paineau M, Mazet ID, Wiedemann-Merdinoglu S, Fabre F, Delmotte F. The Characterization of Pathotypes in Grapevine Downy Mildew Provides Insights into the Breakdown of Rpv3, Rpv10, and Rpv12 Factors in Grapevines. Phytopathology. 2022 Nov;112(11):2329-2340. doi:10.1094/PHYTO-11-21-0458-R.

Introduction

Grapevine downy mildew, caused by the obligate biotrophic oomycete *Plasmopara viticola* (Berk. & M. A. Curt.) Berl. & De Toni, is one of the most destructive oomycetes worldwide (1). *P. viticola* is native to North America, where it infects a large number of wild *Vitis* species (2, 3). Following its initial introduction into European vineyards in the 1870s (4, 5), it spread to all major grape-producing regions of the world (6). The Eurasian wine grape *Vitis vinifera* is highly sensitive to downy mildew and the control of this disease is currently largely based on fungicides. Resistance factors from American and Asian *Vitis* species conferring resistance to downy mildew, and known as 'Rpv' for resistance to *P. viticola*, are currently being used to breed new disease-resistant varieties. More than 30 genetic factors conferring resistance to downy mildew have been identified (7), but only a small number of these factors are currently used in European breeding programs. The so-called Rpv factors are encoded by major QTL located in genomic regions rich in NBS-LRR-like resistance genes (8, 9). These major resistances display monogenic inheritance, but are phenotypically quantitative (or partial), *i.e.*, *P. viticola* strains develop on these varieties, but to a lesser extent than on wild-type varieties. The most widely used resistance factor is Rpv3, which was selected from the species *V. rupestris* (8, 10, 11). The two major haplotypes used in breeding program are Rpv3.1 (Rpv3[299-279]) identified in the variety 'Seibel 4614', and Rpv3.2 (Rpv3[null-279]) identified in the variety 'Munson'('Jaeger 70'). The other major resistance factors currently used in breeding programs are Rpv1 (12), from *Muscadinia rotundifolia*, Rpv10 (13), from *V. amurensis* and Rpv12 (14), also from *V. amurensis*. As in many perennial crops, concerns about the durability of these grapevine resistance factors are magnified by the long duration of breeding schemes (16-17 years (15)) and the lifespan of the plant (about 20-30 years).

Due to its large population size and its capacity for sexual reproduction (16), *P. viticola* has a high evolutionary potential, as illustrated by its rapid adaptation to synthetic fungicides (17–19). The breakdown of the Rpv3.1 factor present in the varieties 'Bianca' and 'Regent' is another example of the rapid adaptation of *P. vitiola* to its host (20–22). Indeed, in this context, virulence emerged within five years on at least three independent occasions, in three different wine-

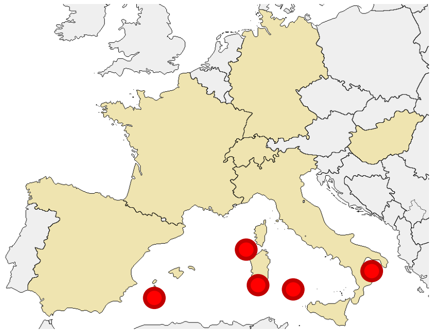
First identification of Avr genes involved in the interaction with grapevine resistance

Paineau et al., 2024, *New Phytol,* 243(4),1490-1505

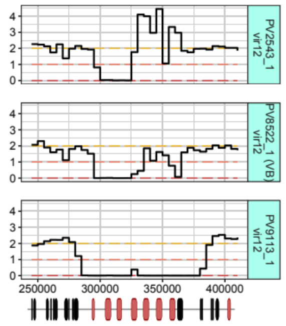
- Rpv3.1 is the most largely deployed resistance
- It triggers localized **necrosis** similar to effector-triggered immunity
- It was recently mapped to a locus containing two NB-LRR genes
- Rapid adaptation pf *Pvi* has been reported in several geographically distant populations over the past decades (Germany, Hungary, Italy, France, etc.)

It suggests a gene-for-gene interaction between grapevine resistance genes and unidentified avr genes

Population genomics - GWAS

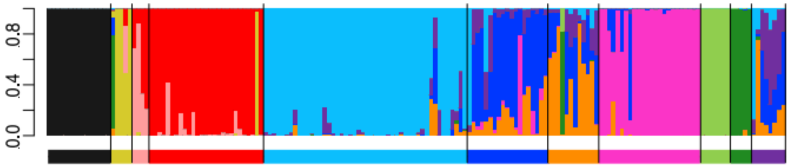


virulent strains from different regions



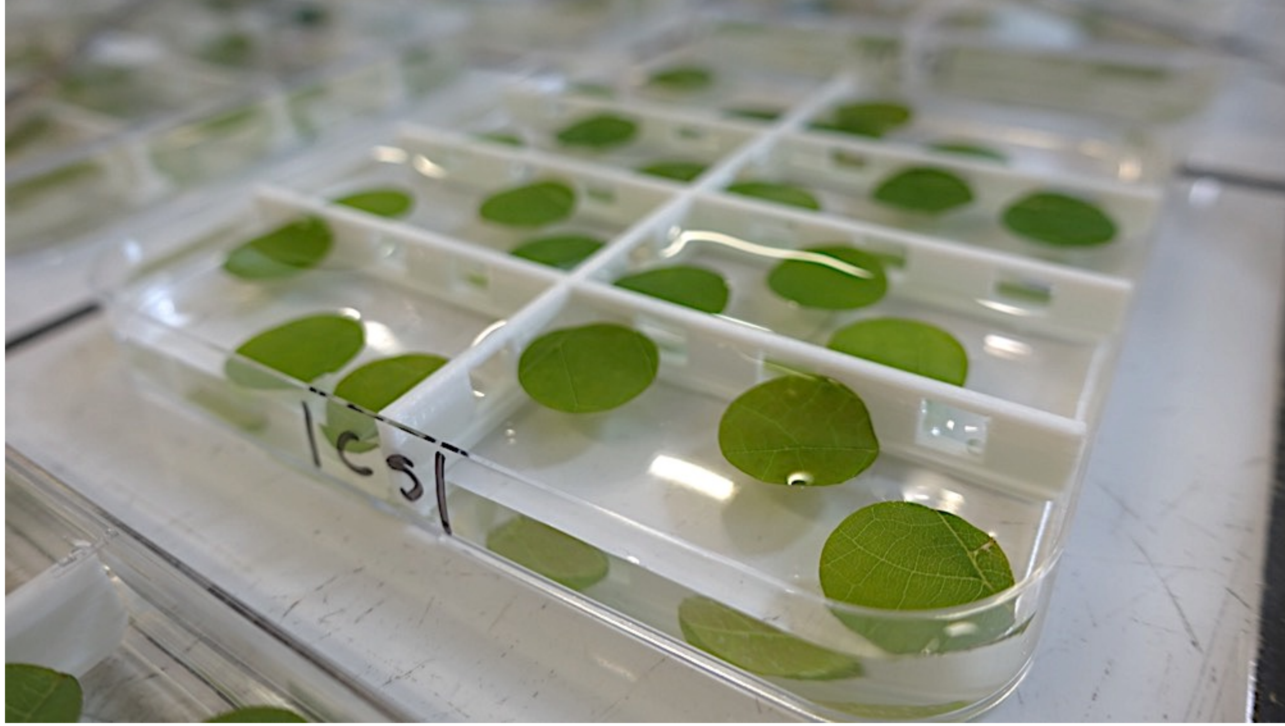
Virulence alleles

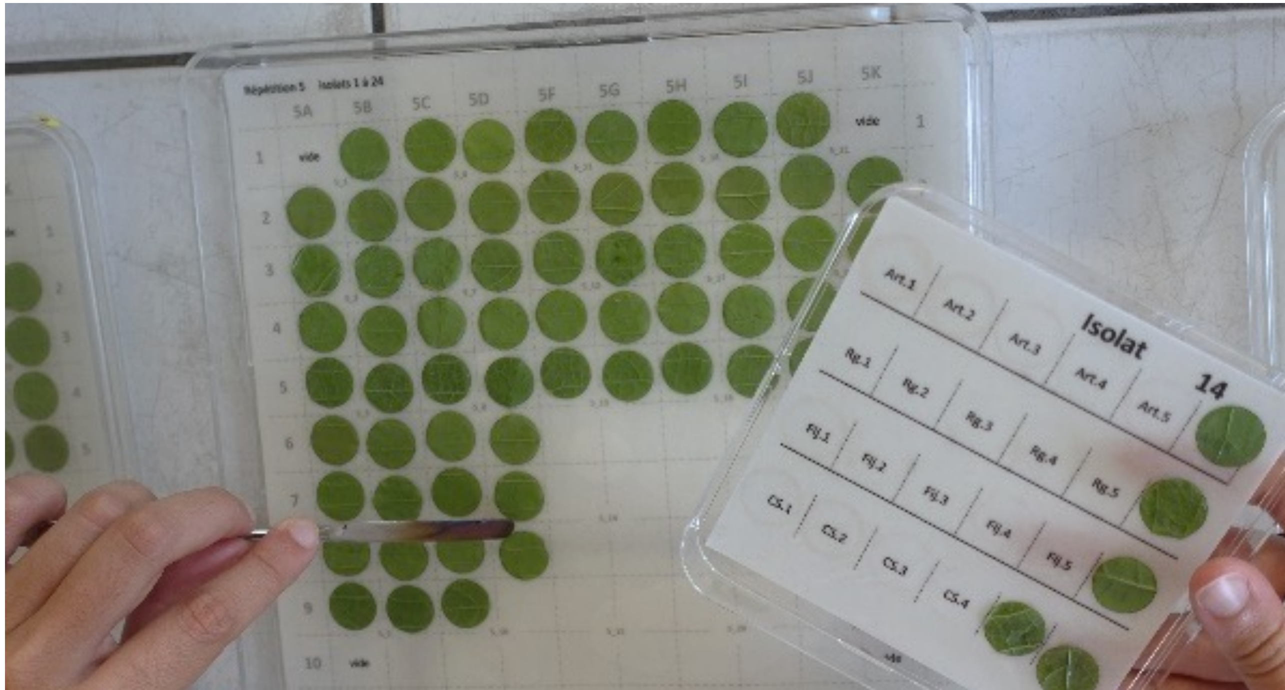
Population structure



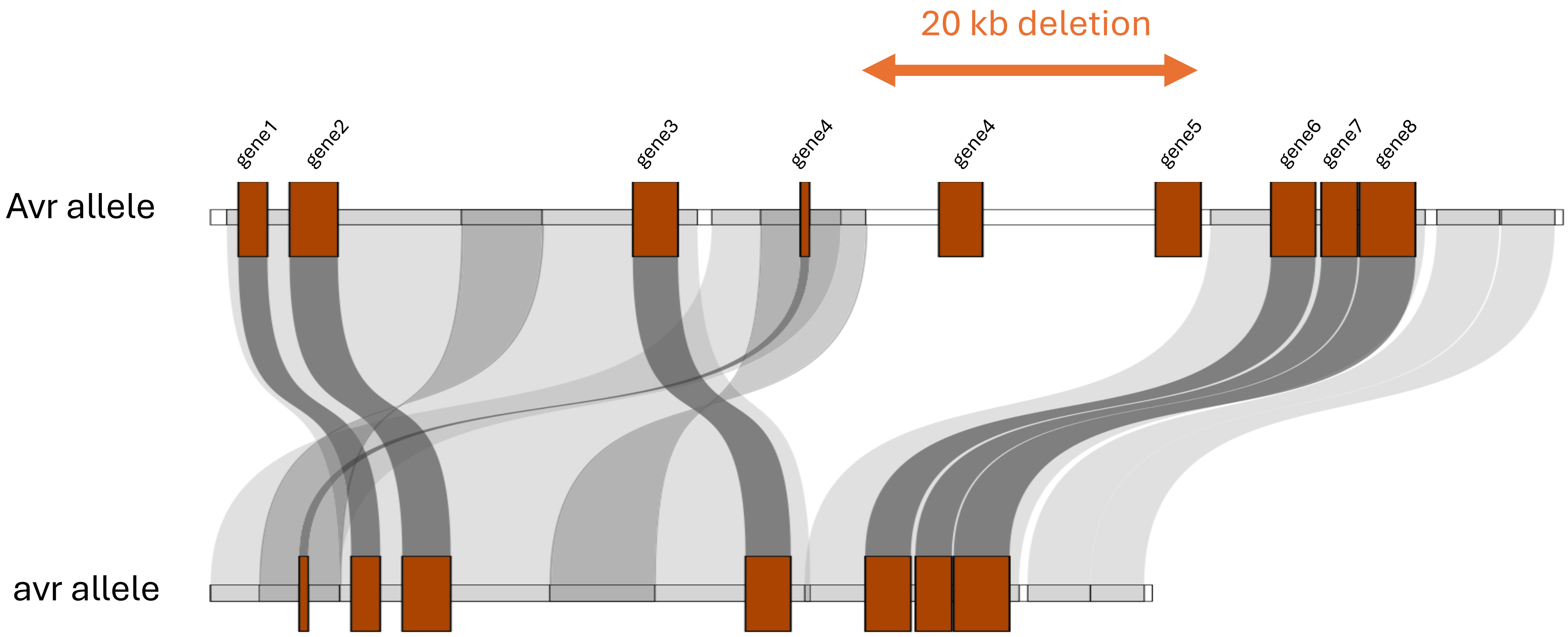
Paineau et al 2024, New Phytol

Paineau et al 2024, New Phytol





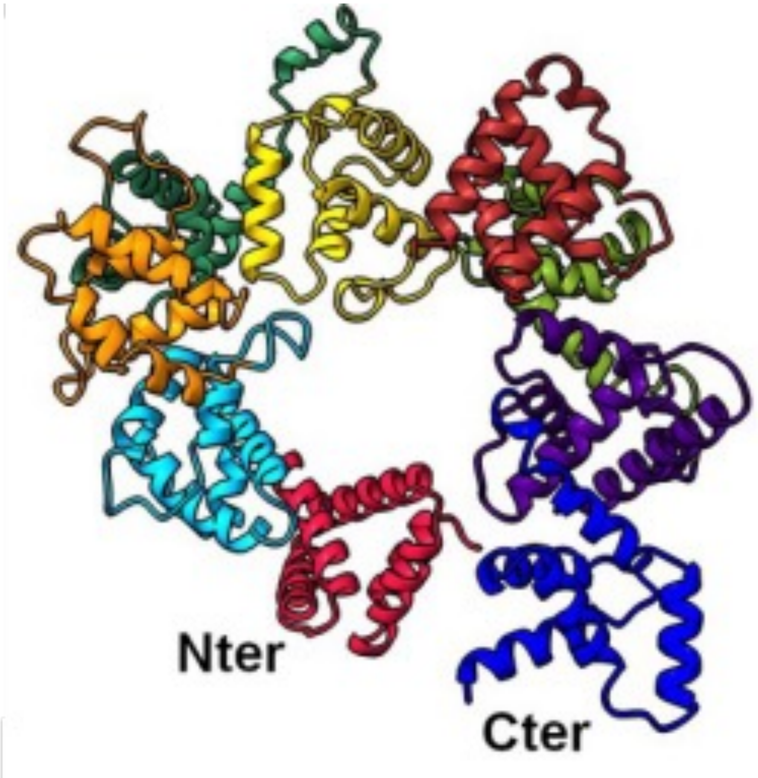
Virulence is significantly associated to a genomic region of P. viticola. A large deletion was detected in the region of interest.



Paineau et al 2024, New Phytol

The candidate genes (g164, g165) encode putative effector proteins

- Protein size of ~**880 amino acids** !
- Presence of a **signal peptide** (EER) => secreted proteins
- Structural similarity with two **RXLRs effectors** of *Phythophthora*
- Agrobacterium-mediated transient expression into leaves of Regent (Rpv3.1+) and the susceptible variety Syrah Both genes induced **cell death in Regent but not in Syrah**.



Paineau et al 2024, New Phytol

Identification of Avr genes involved in the interaction with Rpv10 and Rpv12 resistances

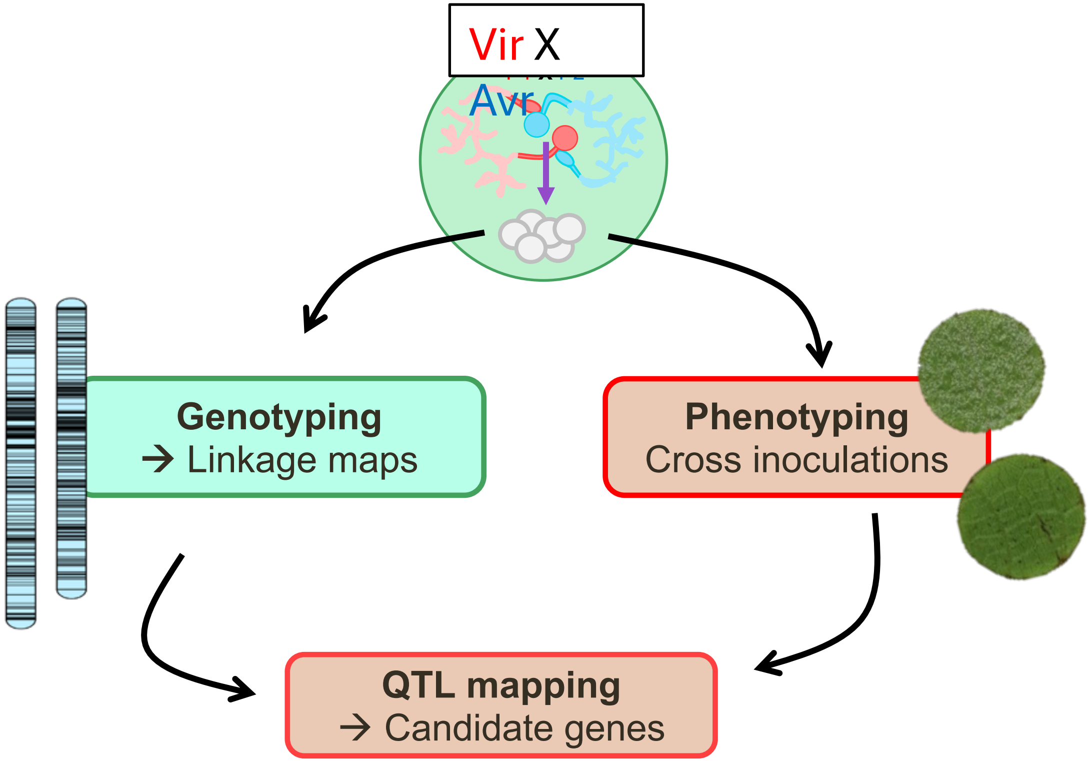
Parallel adaptation and admixture drive the evolution of virulence in the grapevine downy mildew pathogen

Dvorak et al., 2025, ***bioRxiv***

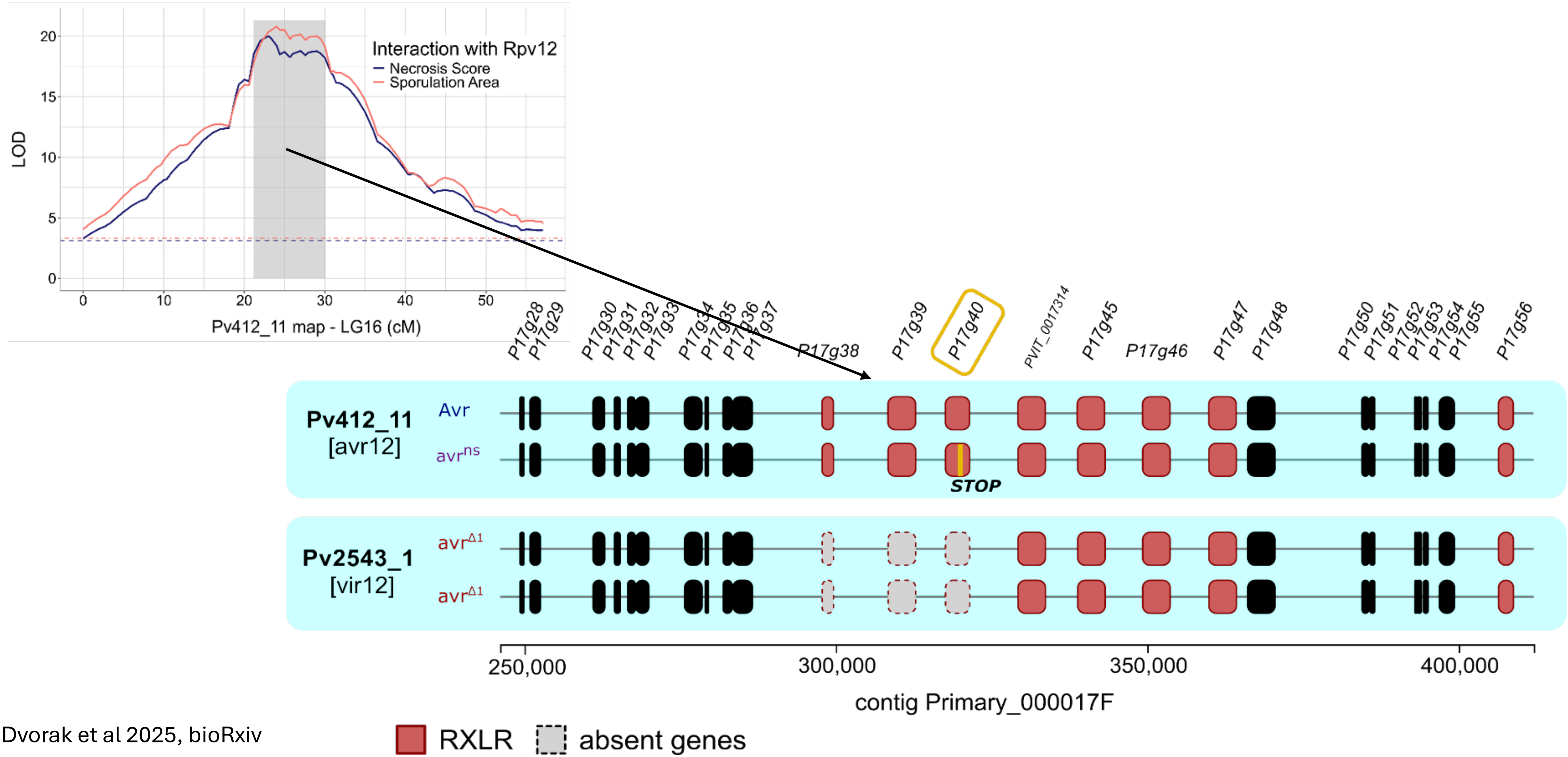
New breakdown of resistance for **Rpv10 and Rpv12**

- Study of genetic determinants of plant-pathogen interactions
- Integrate population genetics approaches to elucidate the evolutionary factors driving the emergence of virulence

Quantitative genomic approach



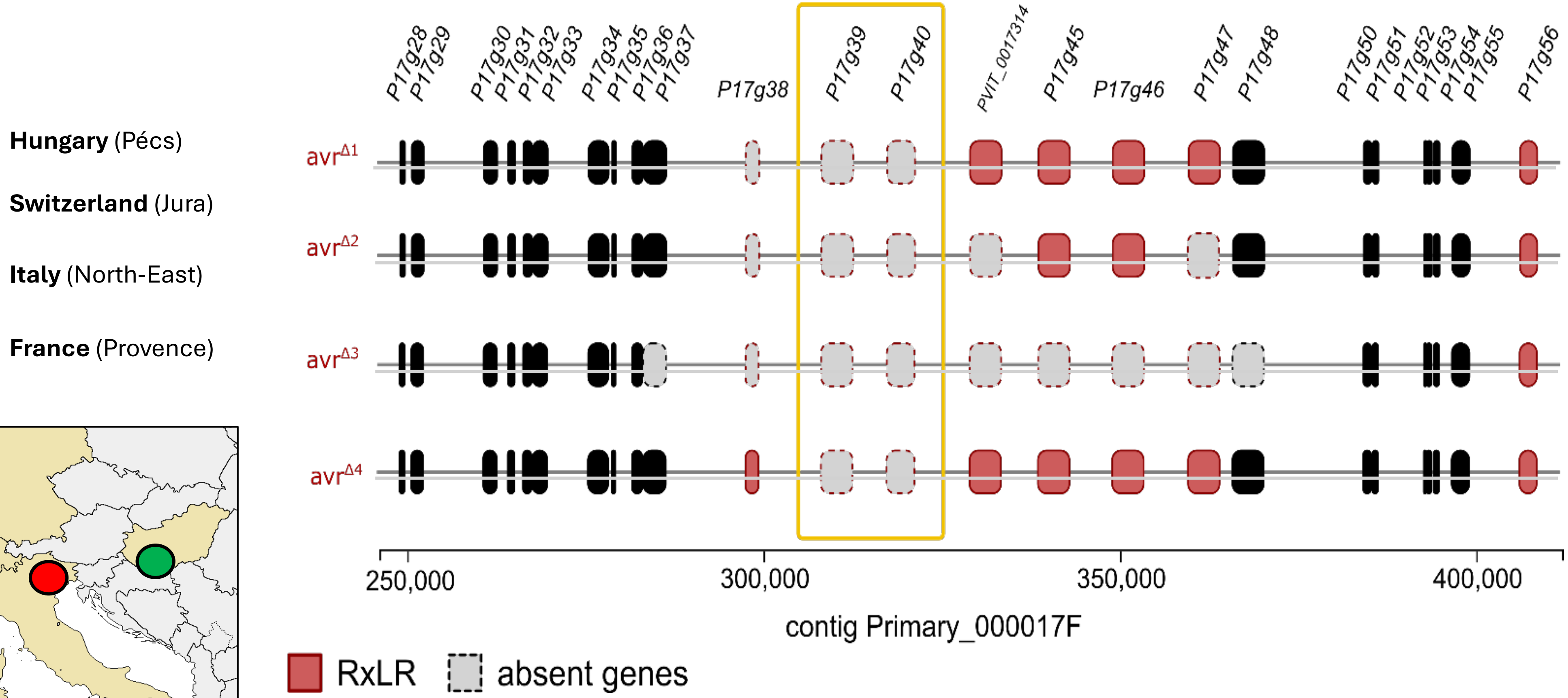
One QTL determines virulence towards Rpv12 associated with homozygous deletions of RXLR genes

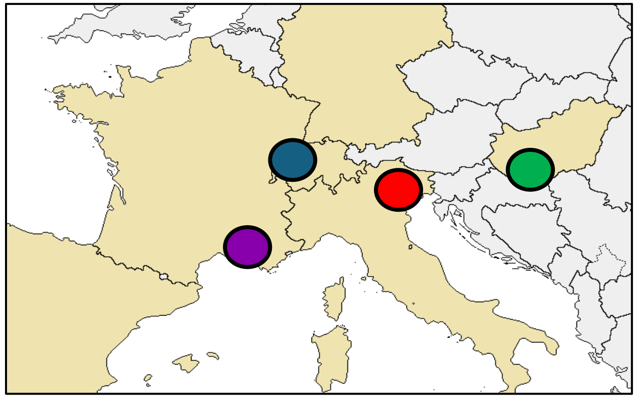


Dvorak et al 2025, bioRxiv

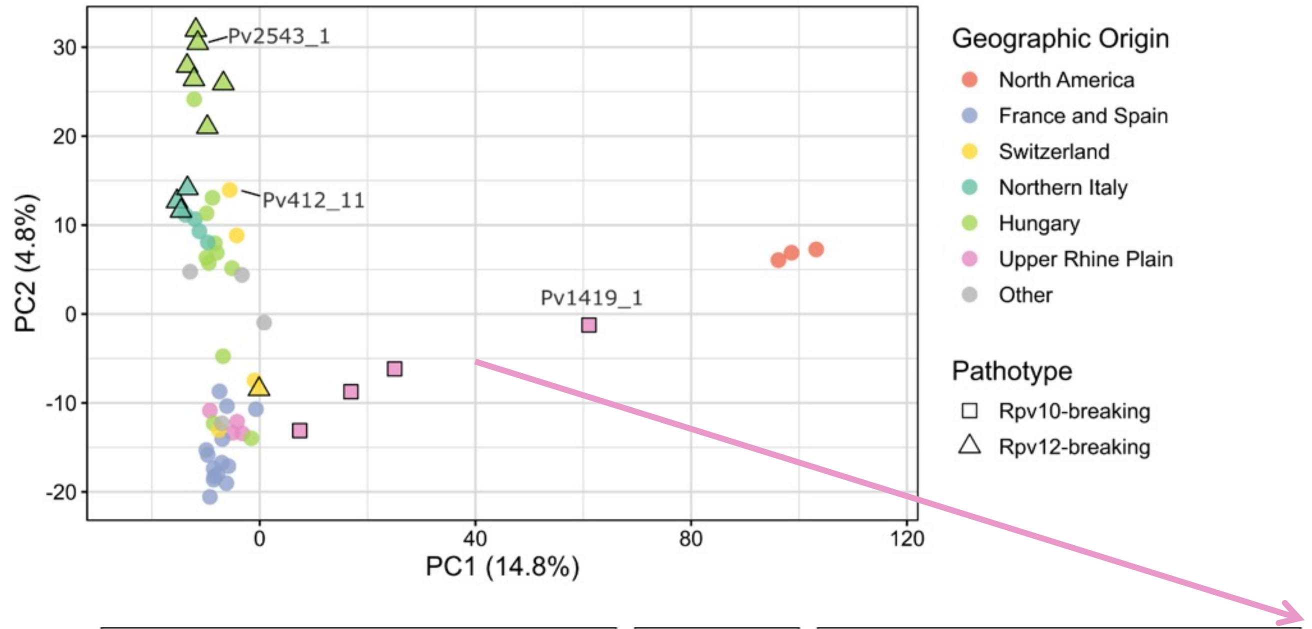
One QTL determines virulence towards Rpv12 in the genome of *P. viticola*

- The virulent parent has a **large homozygous deletion** encompassing 3 RXLR genes in the locus identified
- **Different deletions** sizes : Rpv12 breakdown results from **parallel local adaptations**

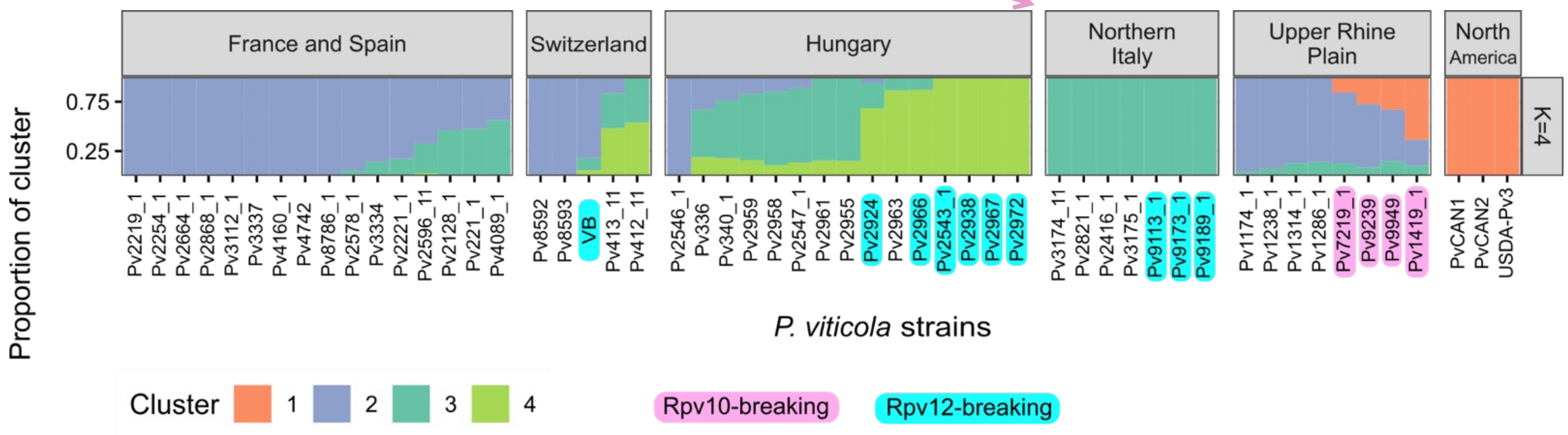




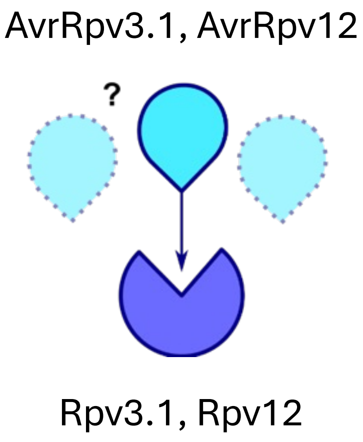
Strains overcoming Rpv10 carry an American admixture



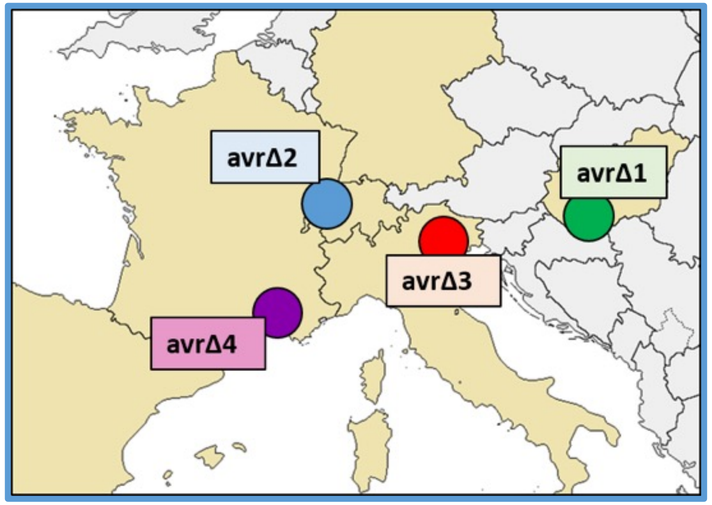
- Strains overcoming Rpv10 all originate from the Upper Rhine Plain
- Theey show variable level of admixture with a North American genetic background

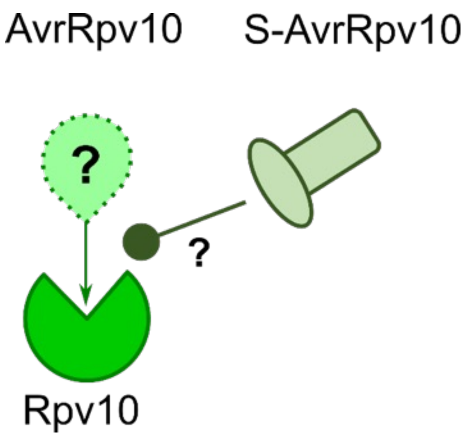


Virulence twoards R genes : distinct mechanisms and evolutionnary pathways

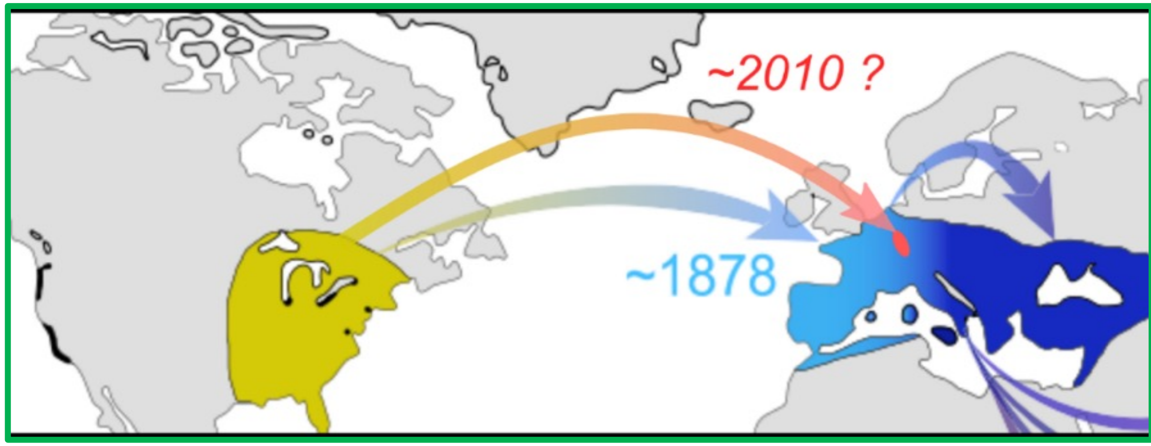


- Breakdown of **Rpv3.1 Rpv12** by **loss of Avr** factor (recessive)
- **Parallel adaptations** upon the recent deployment in Europe





- Partial breakdown of **Rpv10** by a potential **gain of suppressor** (dominant)
- Adaptation facilitated by **admixture** (introduction of new alleles in Europe)



Dvorak et al 2025, BioRxiv

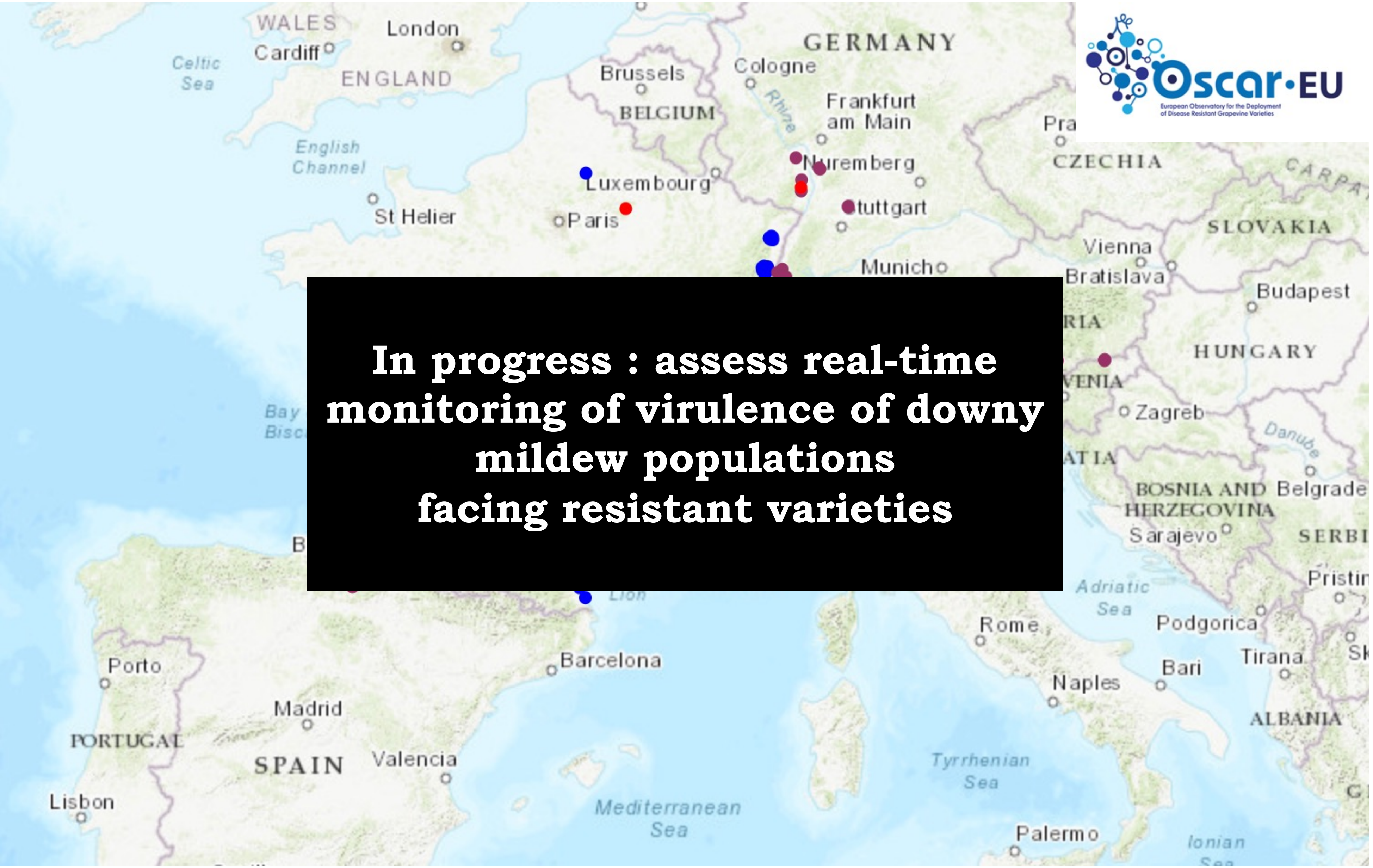
A European-wide monitoring of grapevine disease-resistant varieties

grapebreed 4 IPM

> 60 parcels in production are included at the EU level

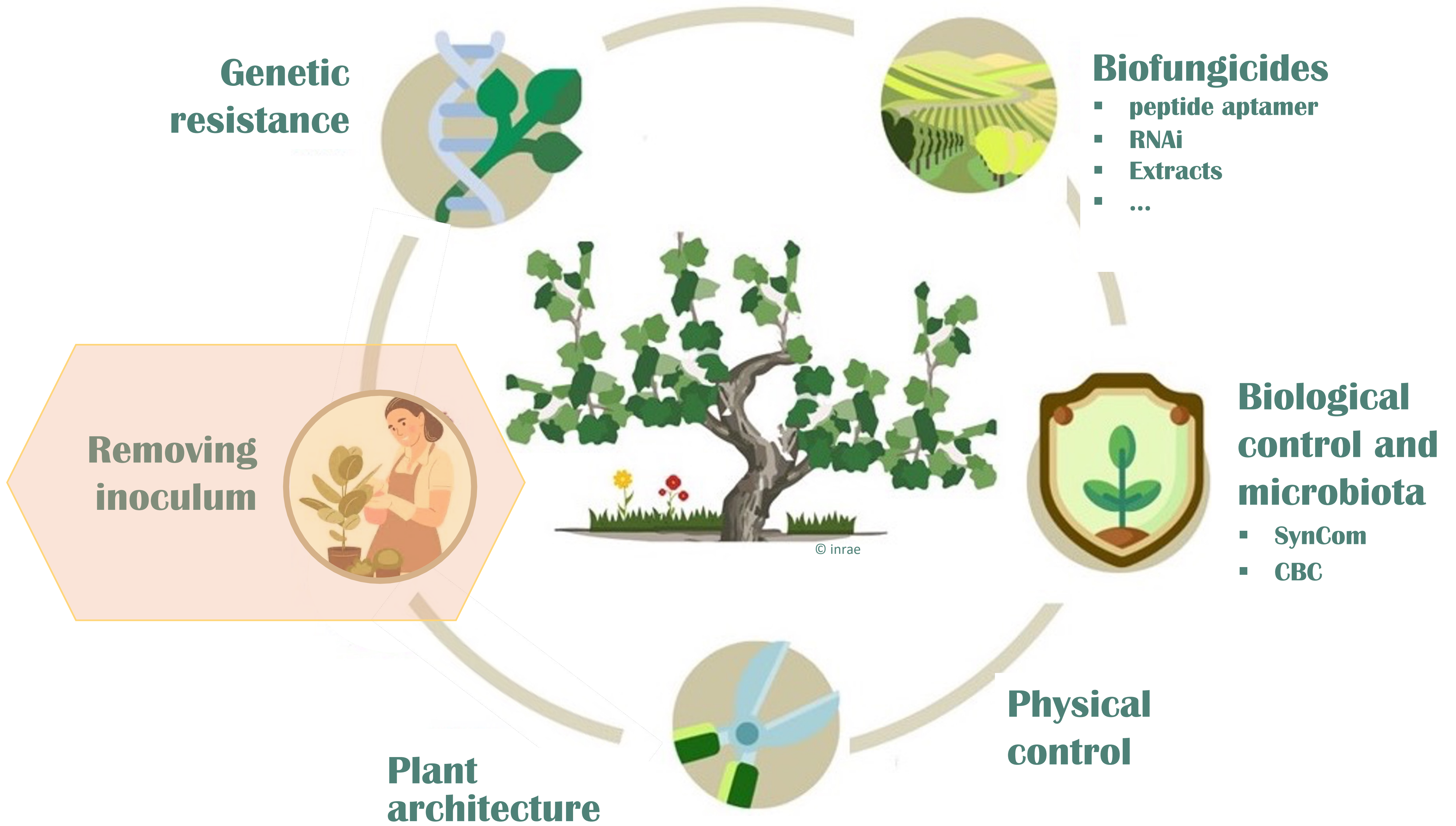
In France (2024)

- 186 fields in production
- >100 localities
- 36 partners
- 32 varieties



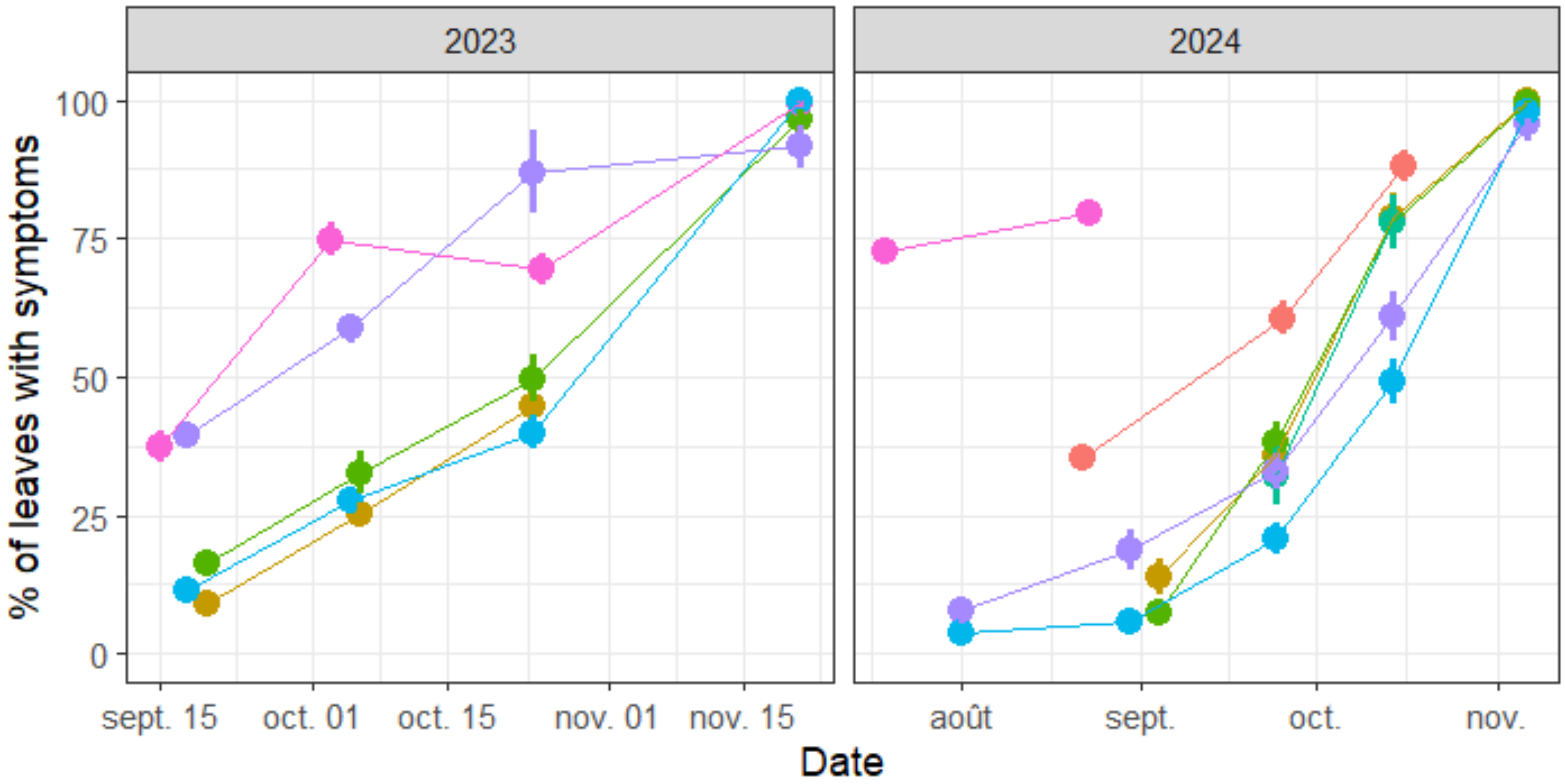
In progress : assess real-time monitoring of virulence of downy mildew populations facing resistant varieties

Oscar·EU
European Observatory for the Deployment of Disease Resistant Grapevine Varieties



Genetic resistance
Biofungicides
▪ peptide aptamer
▪ RNAi
▪ Extracts
▪ …
Removing inoculum
© inrae
Biological control and microbiota
▪ SynCom
▪ CBC
Physical control
Plant architecture


Large epidemics in autumn, whatever the epidemics during the season

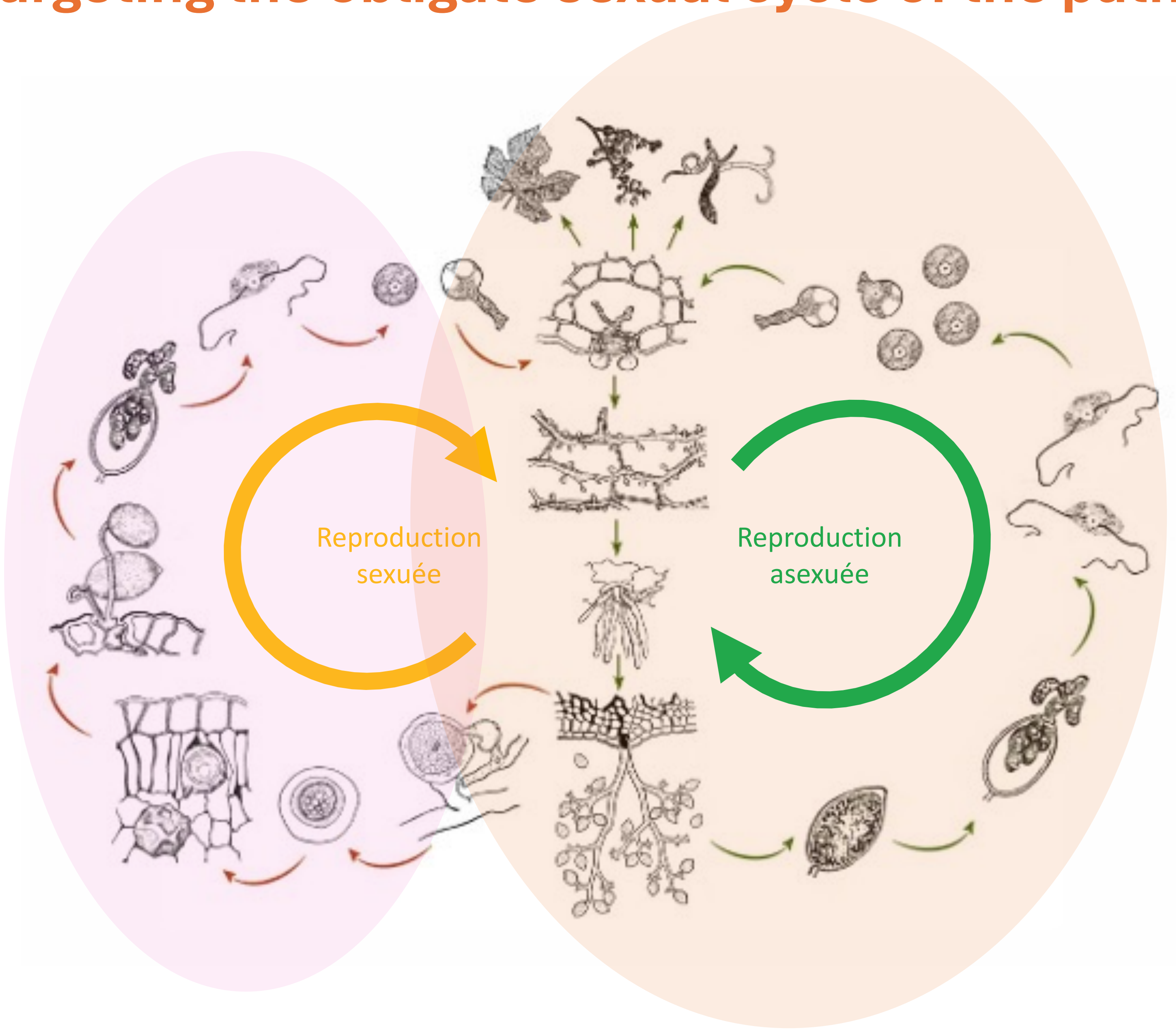


In 2024, oospore formation takes place between September 29 and October 16

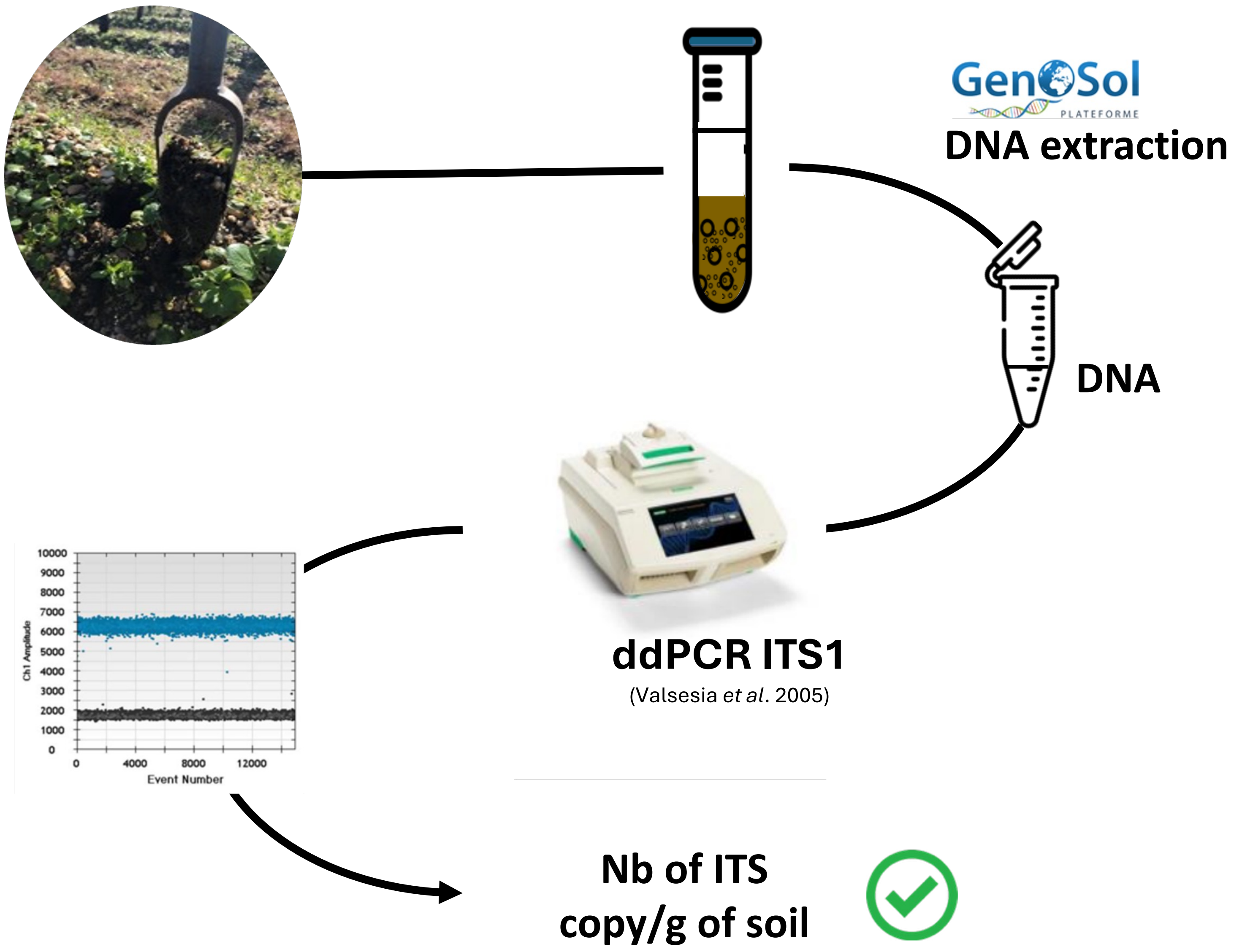
Develop a prophylaxis targeting the obligate sexual cycle of the pathogen

disrupting sexual cycle by

- Limiting primary infections
- Removing infected crop residues
- Limiting oospores formation



We developed a new **ddPCR method** for quantifying **oospores reservoirs in vineyard**

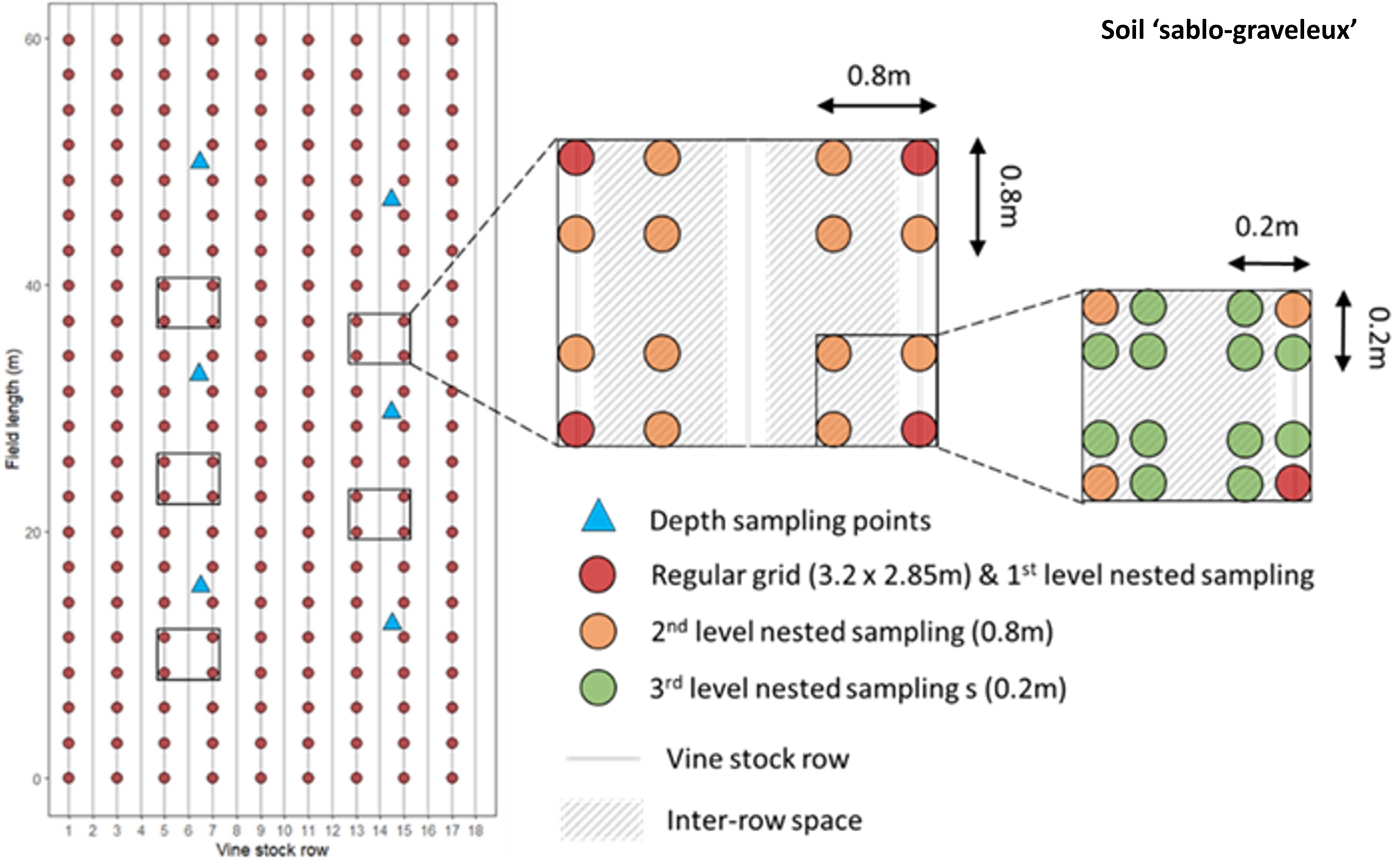


feb. 2022, 318 soil samples collected

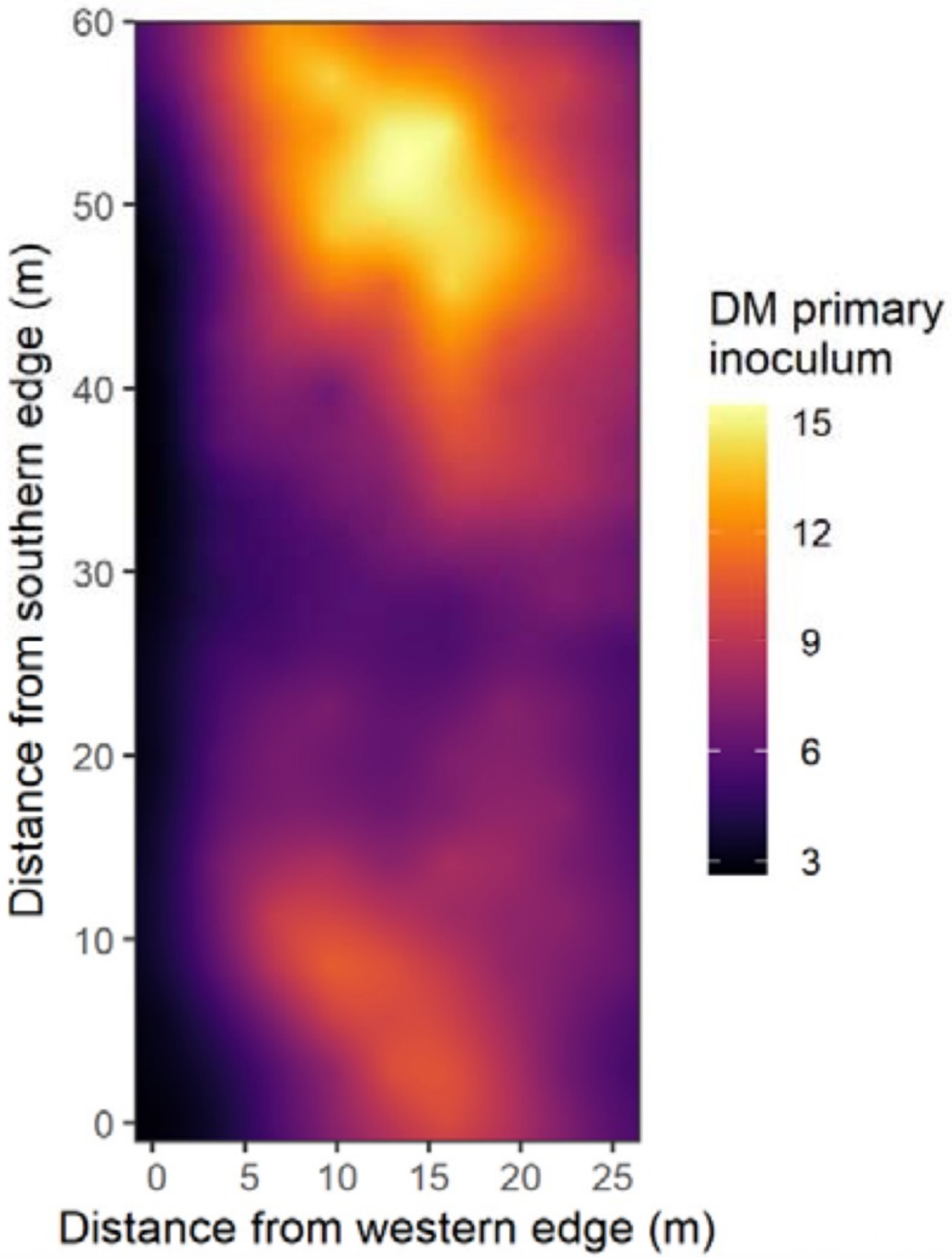
Merlot plot

0,18 ha

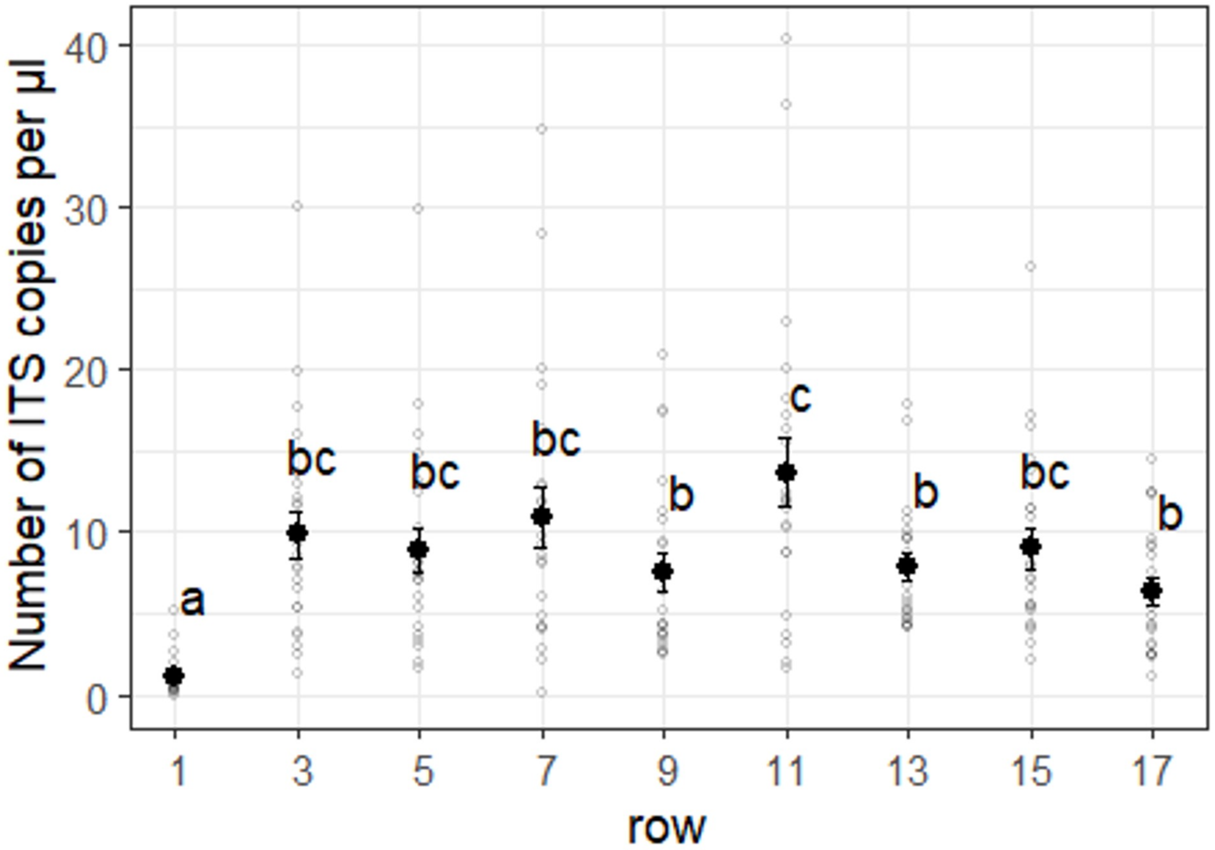
Soil 'sablo-graveleux'



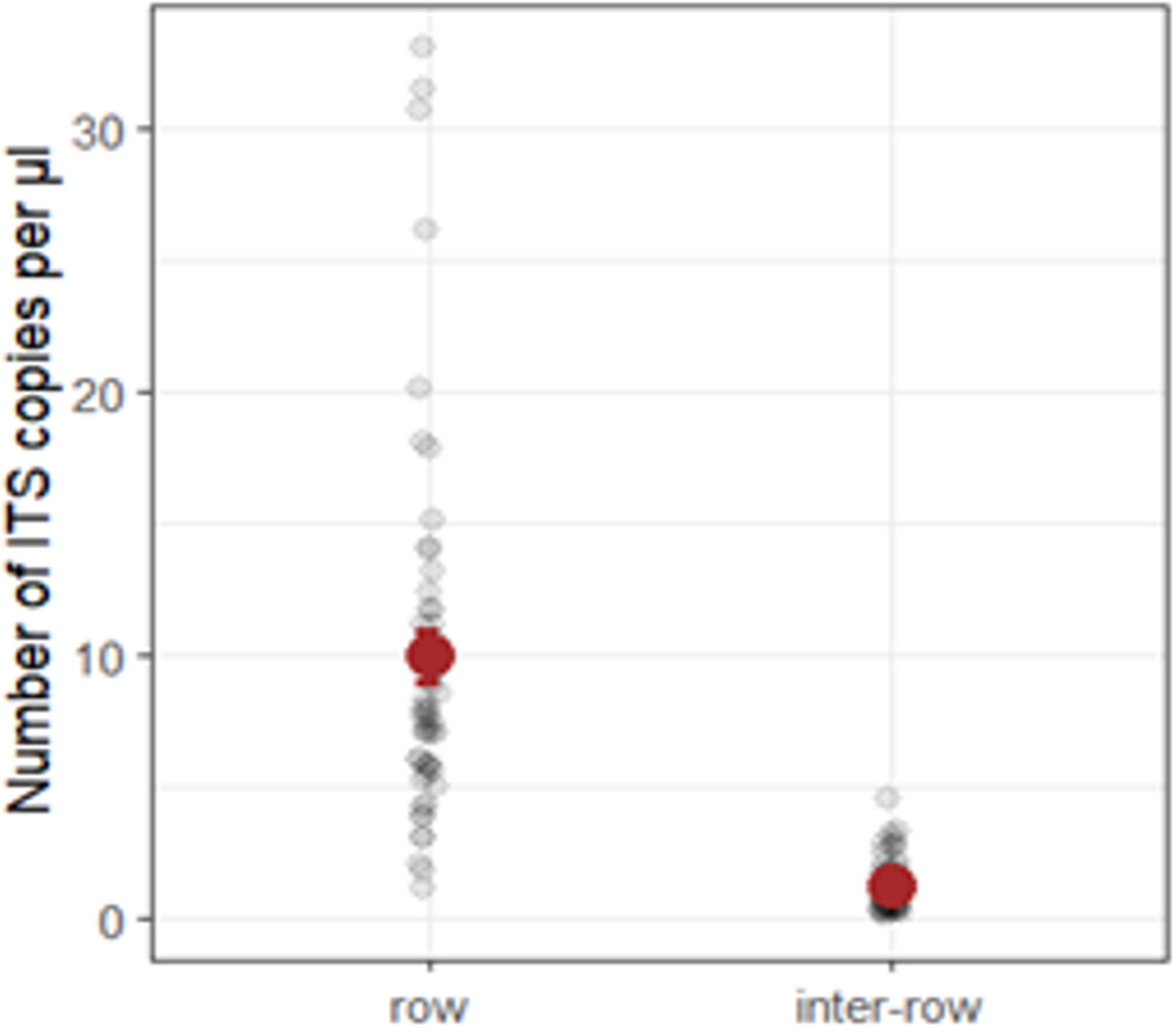
Direct quantitative assessment using digital droplet PCR and field-scale spatial distribution of *Plasmopara viticola* oospores in vineyard soil
Charlotte Poeydebat, Eva Courchinoux, Isabelle D. Mazet, Marie Rodriguez, AlexandreChataigner, Mélanie Lelièvre, Jean-Pascal Goutouly, Jean-Pierre Rossi, Marc Raynal, Laurent Delière, François Delmotte
bioRxiv 2024.07.29.605284; doi: https://doi.org/10.1101/2024.07.29.605284. /In press in AEM



- High spatial variability within plots
- Spatial autocorrelation < 10 meters
- Effect of row distribution



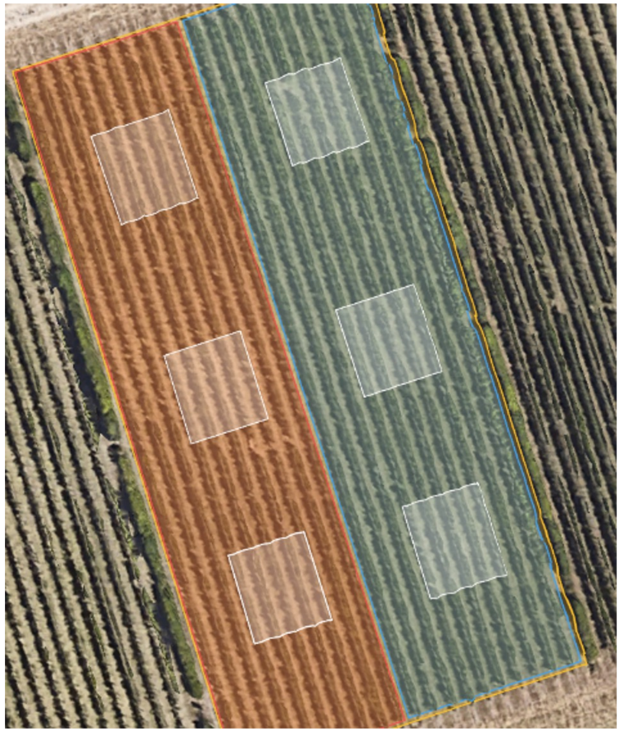
=> 5 times more inoculum (oospores) on the row

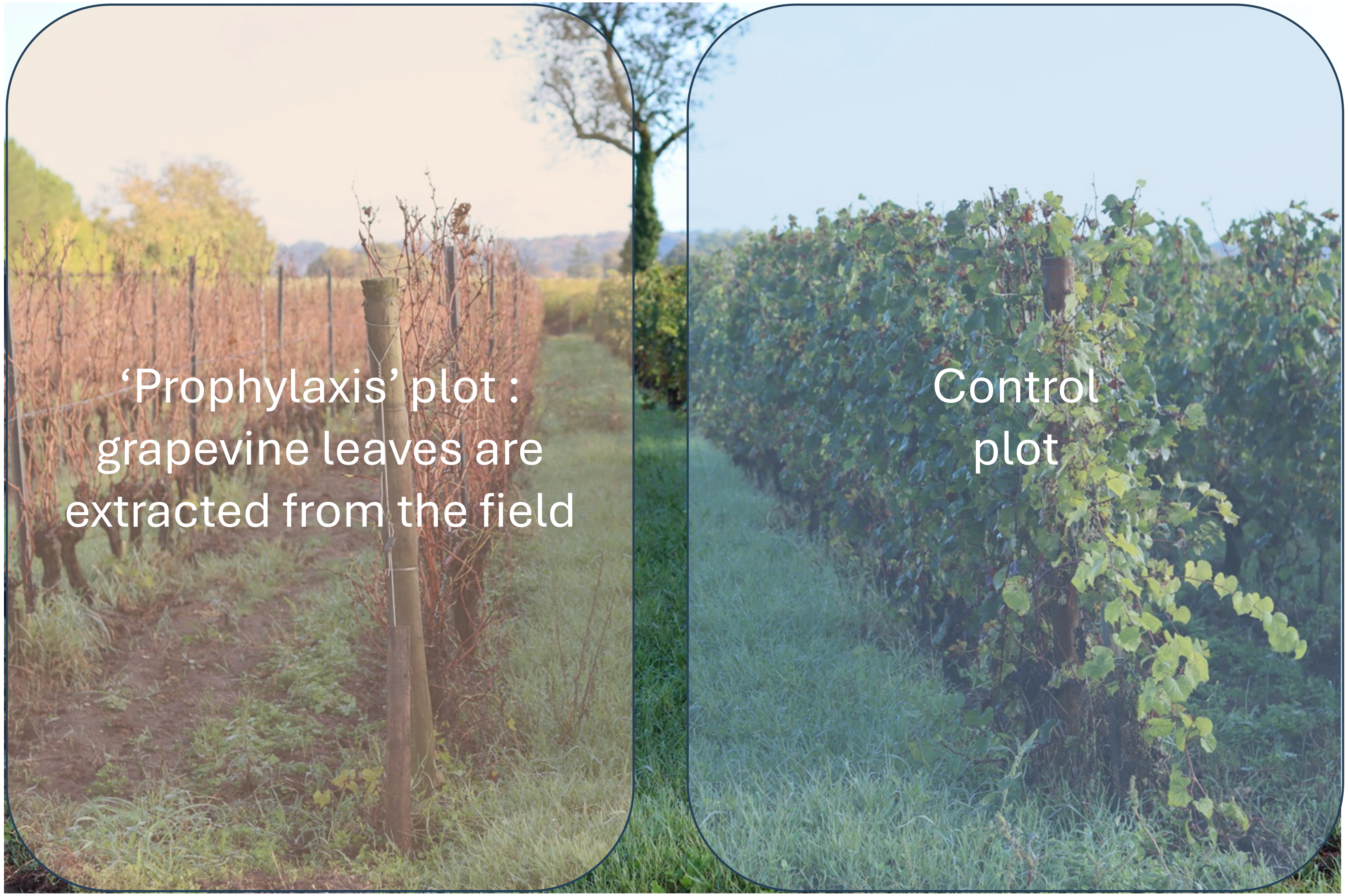


An experiment to assess the efficiency of removing primary inoculum on grapevine downy mildew epidemics

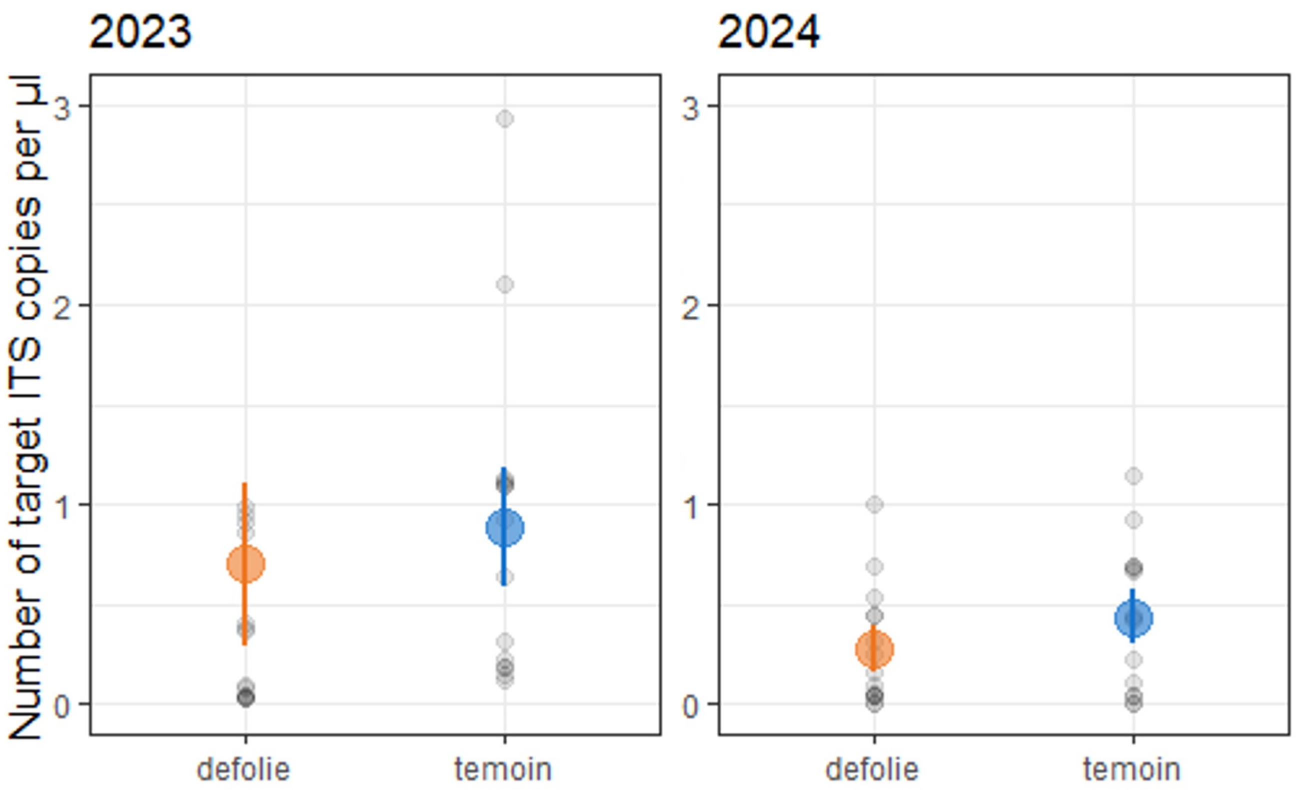
inoculum removal

control

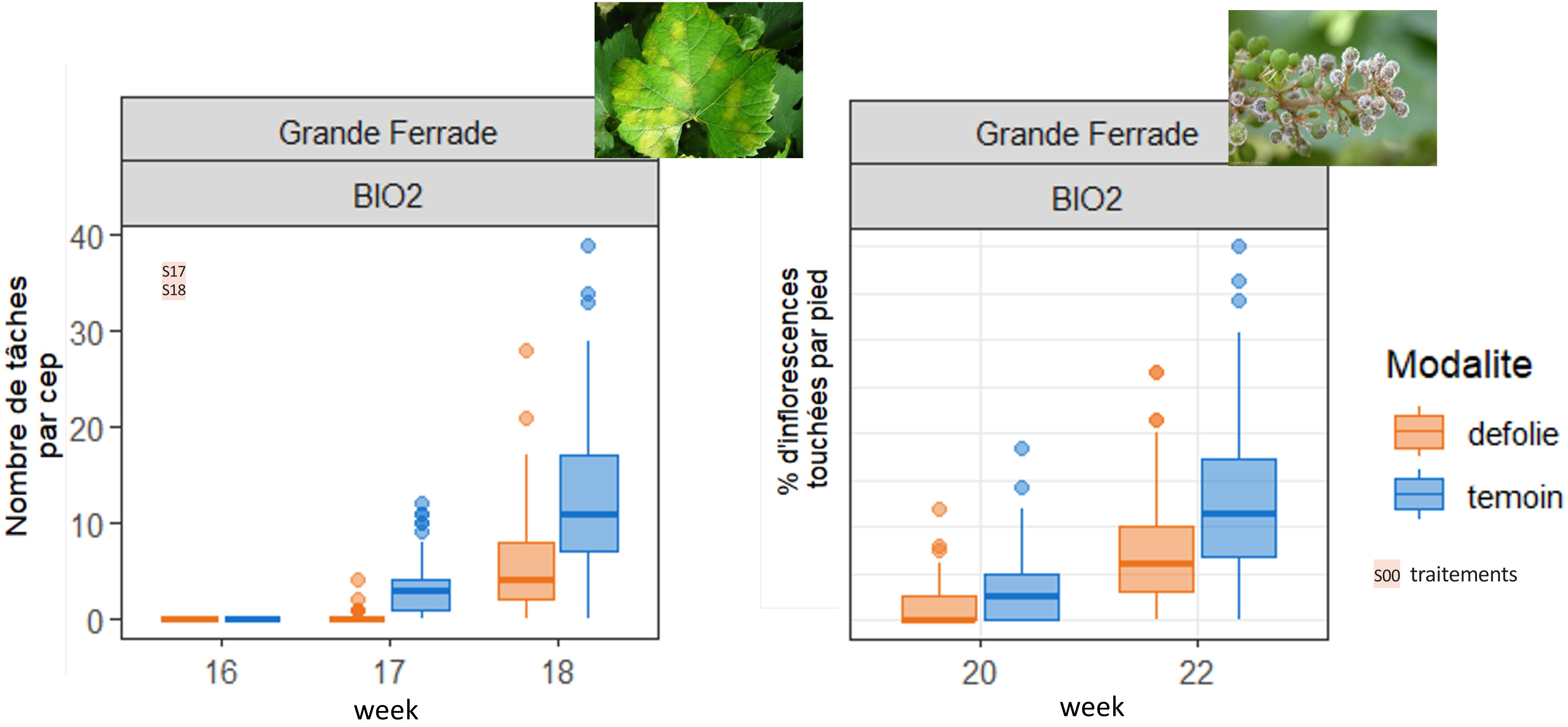




A reduction in the amount of primary inoculum in the soil

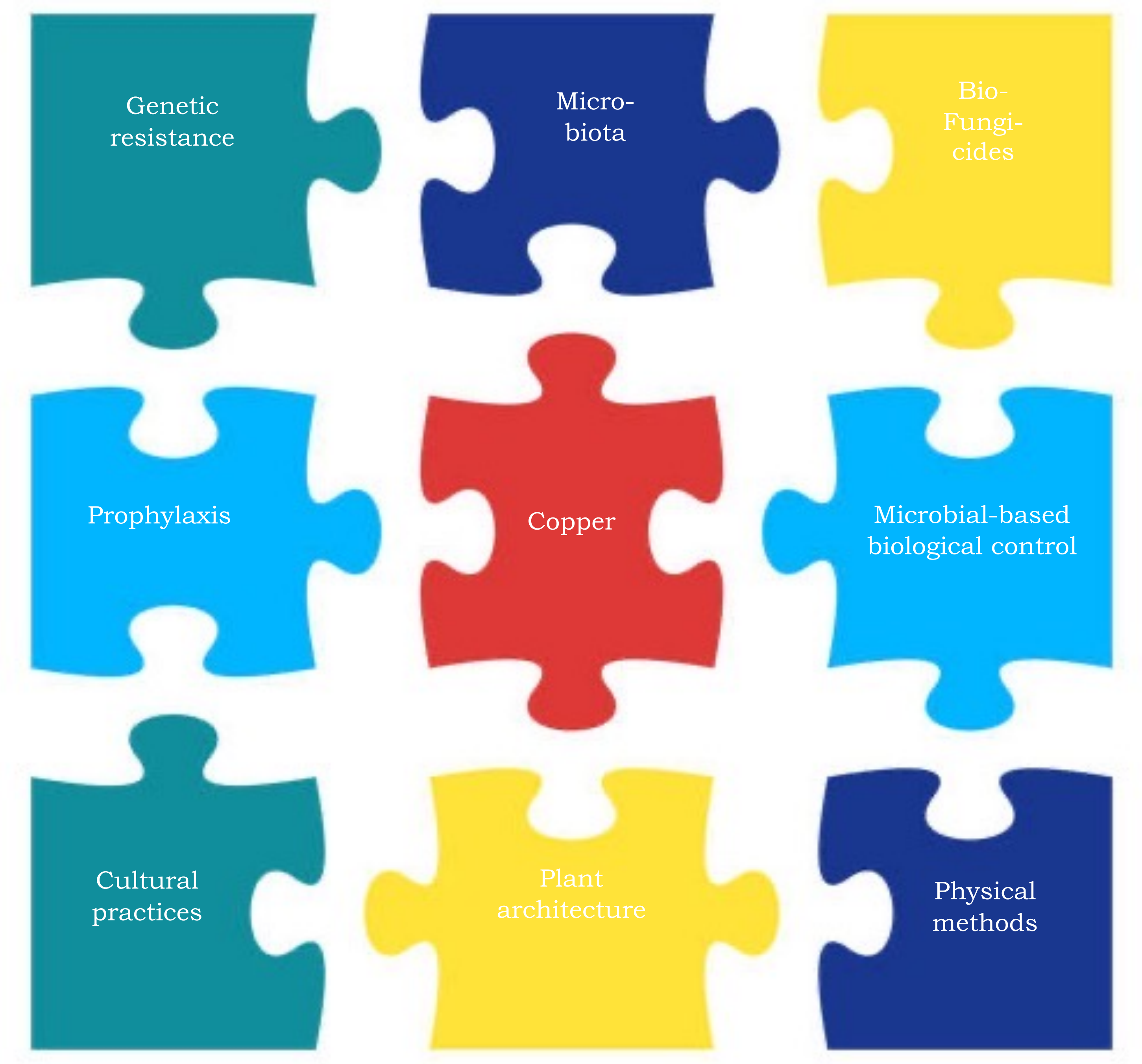


> 50% reduction in downy mildew on leaves and bunches in 2024



Gene
resistan

Removing inoculum

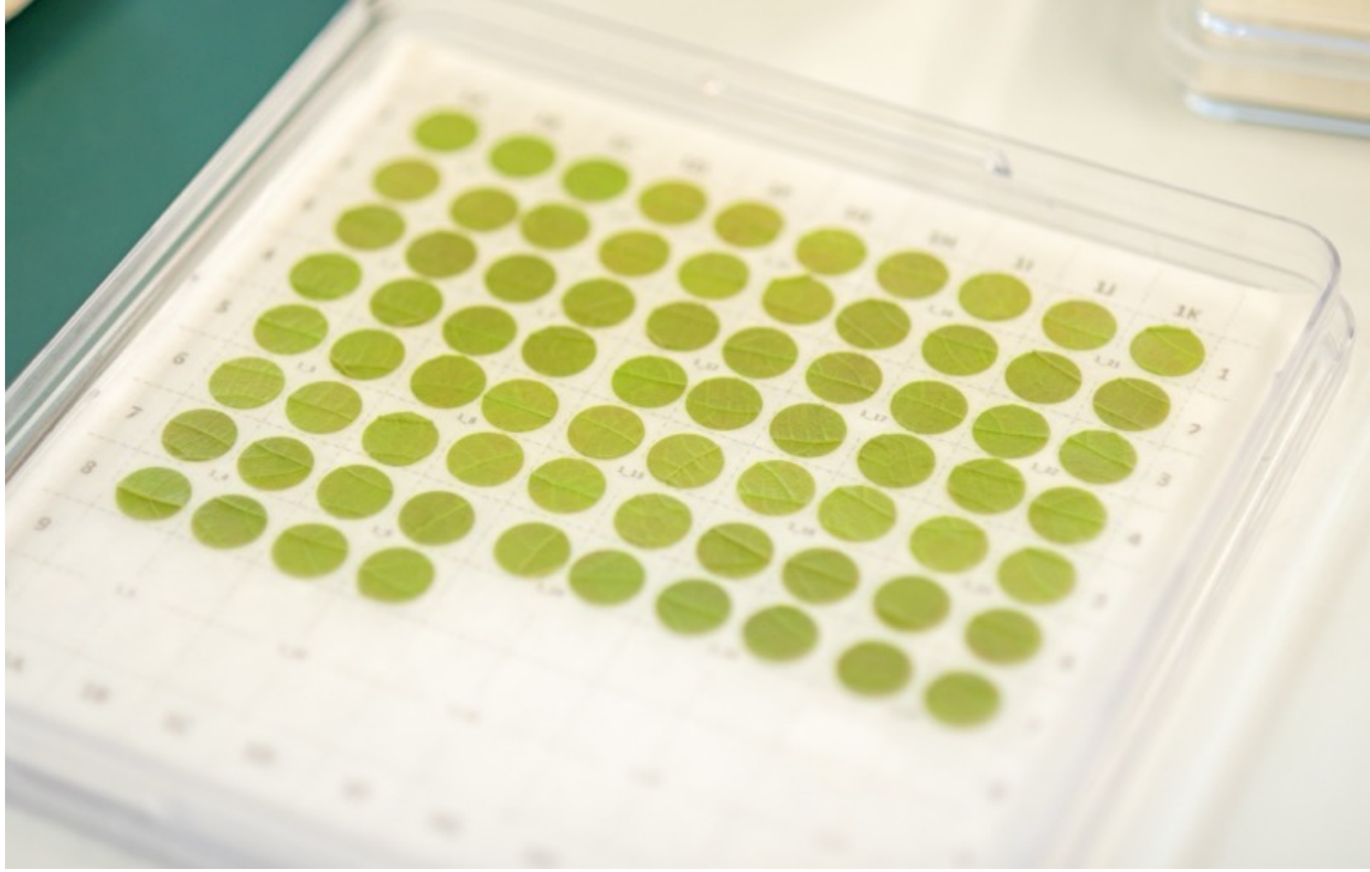


gicides
e aptamer
ts

Biological control and microbiota

- SynCom
- CBC

Carole Couture, inrae
Laurent Delière, inrae
Isabelle Demeaux, inrae
Frédéric Fabre, inrae
Pere Mestre, inrae
Anne-Sophie Miclot, inrae
Charlotte Poyedebat, bsa
Benoit Laurent - ifv
Xavier Burgun ifv
Lucie Andrianasolonirina
Paige Breen
Eva Courchinoux
Yann Dussert
Etienne Dvorak
Manon Paineau
Laura Marolleau
Julie Martinez
Marie Rodriguez



Thank you for your attention