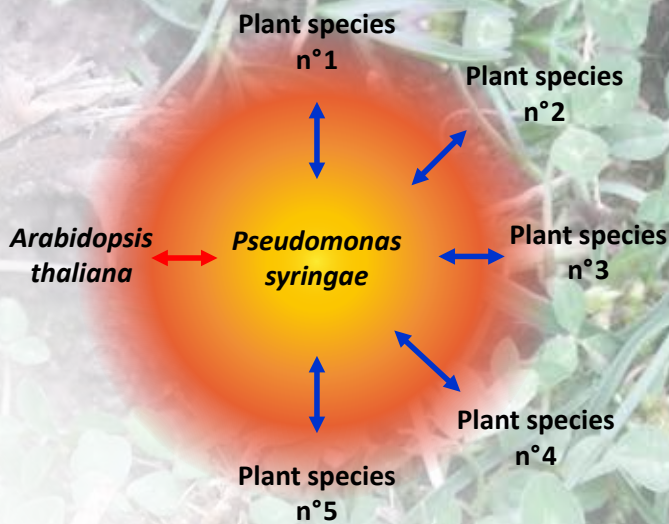


# The long-term maintenance of a resistance polymorphism through diffuse interactions

**P**lant resistance - *R genes* - are a crucial component in plant defence against pathogens. Although *R genes* often fail to provide durable resistance in an agricultural context, they frequently persist as long-lived balanced polymorphisms in nature. Standard theory explains the maintenance of such polymorphisms through a balance of the costs and benefits of resistance and virulence in a tightly coevolving host–pathogen pair. However, many plant–pathogen interactions lack such specificity.

Whether, and how, balanced polymorphisms are maintained in diffusely interacting species is unknown. Here we identify a naturally interacting *R gene* and effector pair in *Arabidopsis thaliana* and its facultative plant pathogen, *Pseudomonas syringae*. The protein encoded by the *R gene* *RPS5* recognizes an AvrPphB homologue (AvrPphB2) and exhibits a balanced polymorphism that has been maintained for over 2 million years. Consistent with the presence of an ancient balanced polymorphism, the *R gene* confers a benefit when plants are infected with *P. syringae* carrying *avrPphB2* but also incurs a large cost in the absence of infection. *RPS5* alleles are maintained at intermediate frequencies in populations globally, suggesting ubiquitous selection for resistance.

However, the presence of *P. syringae* carrying *avrPphB* is probably insufficient to explain the *RPS5* polymorphism. First, *avrPphB* homologues occur at very low frequencies in *P. syringae* populations on *A. thaliana*. Second, AvrPphB only rarely confers a virulence benefit to *P. syringae* on *A. thaliana*. Instead, we find evidence that selection for *RPS5* involves multiple non-homologous effectors and multiple pathogen species. These results and an associated model suggest that the *R gene* polymorphism in *A. thaliana* may not be maintained through a tightly coupled interaction involving a single coevolved *R gene* and effector pair. More likely, the stable polymorphism is maintained through complex and diffuse community-wide interactions.



**Fig.:** Impact of plant communities on the evolution of *R genes* in *A. thaliana*