



# Peer Community In Evolutionary Biology

## The pace of pathogens' adaptation to their host plants

**Benoit Moury** based on peer reviews by **Benoit Moury** and 1 anonymous reviewer

Frederic Suffert, Henriette Goyeau, Ivan Sache, Florence Carpentier, Sandrine Gelisse, David Morais, Ghislain Delestre (2017) Epidemiological trade-off between intra- and interannual scales in the evolution of aggressiveness in a local plant pathogen population. Missing preprint\_server, ver. Missing article\_version, peer-reviewed and recommended by Peer Community in Evolutionary Biology. [10.1101/151068](https://doi.org/10.1101/151068)

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Because of their shorter generation times and larger census population sizes, pathogens are usually ahead in the evolutionary race with their hosts. The risks linked to pathogen adaptation are still exacerbated in agronomy, where plant and animal populations are not freely evolving but depend on breeders and growers, and are usually highly genetically homogeneous. As a consequence, the speed of pathogen adaptation is crucial for agriculture sustainability. Unraveling the time scale required for pathogens' adaptation to their hosts would notably greatly improve our estimation of the risks of pathogen emergence, the efficiency of disease control strategies and the design of epidemiological surveillance schemes. However, the temporal scale of pathogen evolution has received much less attention than its spatial scale [1]. In their study of a wheat fungal disease, Suffert et al. [2] reached contrasting conclusions about the pathogen adaptation depending on the time scale (intra- or inter-annual) and on the host genotype (sympatric or allopatric) considered, questioning the experimental assessment of this important problem. Suffert et al. [2] sampled two pairs of *Zymoseptoria tritici*\* (the causal agent of septoria leaf blotch) sub-populations in a bread wheat field plot, representing (i) isolates collected at the beginning or at the end of an epidemic in a single growing season (2009-2010 intra-annual sampling scale) and (ii) isolates collected from plant debris at the end of growing seasons in 2009 and in 2015 (inter-annual sampling scale). Then, they measured in controlled conditions two aggressiveness traits of the isolates of these four *Z. tritici*\* sub-populations, the latent period and the lesion size on leaves, on two wheat cultivars. One of the cultivars was considered as "sympatric" because it was at the source of the studied isolates and was predominant in the growing area before the experiment, whereas the other cultivar was considered as "allopatric" since it replaced the previous one and became predominant in the

growing area during the sampling period. On the sympatric host, at the intra-annual scale, they observed a marginally-significant decrease in latent period and a significant decrease of the between-isolate variance for this trait, which are consistent with a selection of pathogen variants with an enhanced aggressiveness. In contrast, at the inter-annual scale, no difference in the mean or variance of aggressiveness trait values was observed on the sympatric host, suggesting a lack of pathogen adaptation. They interpreted the contrast between observations at the two time scales as the consequence of a trade-off for the pathogen between a gain of aggressiveness after several generations of asexual reproduction at the intra-annual scale and a decrease of the probability to reproduce sexually and to be transmitted from one growing season to the next. Indeed, at the end of the growing season, the most aggressive isolates are located on the upper leaves of plants, where the pathogen density and hence probably also the probability to reproduce sexually, is lower. On the allopatric host, the conclusion about the pathogen stability at the inter-annual scale was somewhat different, since a significant increase in the mean lesion size was observed (isolates corresponding to the intra-annual scale were not checked on the allopatric host). This shows the possibility for the pathogen to evolve at the inter-annual scale, for a given aggressiveness trait and on a given host. In conclusion, Suffert et al.'s [2] study emphasizes the importance of the experimental design in terms of sampling time scale and host genotype choice to analyze the pathogen adaptation to its host plants. It provides also an interesting scenario, at the crossroad of the pathogen's reproduction regime, niche partitioning and epidemiological processes, to interpret these contrasted results. Pathogen adaptation to plant cultivars with major-effect resistance genes is usually fast, including in the wheat-\*Z. tritici\* system [3]. Therefore, this study will be of great help for future studies on pathogen adaptation to plant partial resistance genes and on strategies of deployment of such resistance at the landscape scale.

### **References:**

- [1] Penczykowski RM, Laine A-L and Koskella B. 2016. Understanding the ecology and evolution of host-parasite interactions across scales. *Evolutionary Applications*, 9: 37–52. doi: [10.1111/eva.12294](<https://doi.org/10.1111/eva.12294>)
- [2] Suffert F, Goyeau H, Sache I, Carpentier F, Gelisse S, Morais D and Delestre G. 2017. Epidemiological trade-off between intra- and interannual scales in the evolution of aggressiveness in a local plant pathogen population. *bioRxiv*, 151068, ver. 3 of 12th November 2017. doi: [10.1101/151068](<https://doi.org/10.1101/151068>)
- [3] Brown JKM, Chartrain L, Lasserre-Zuber P and Saintenac C. 2015. Genetics of resistance to \*Zymoseptoria tritici\* and applications to wheat breeding. *Fungal Genetics and Biology*, 79: 33–41. doi: [10.1016/j.fgb.2015.04.017](<https://doi.org/10.1016/j.fgb.2015.04.017>)

## **Reviews**

### **Evaluation round #1**

DOI or URL of the preprint: [10.1101/151068](https://doi.org/10.1101/151068)

Version of the preprint: 1

### **Authors' reply, 18 October 2017**

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## Decision by **Benoit Moury**, posted 02 September 2017

### Revise

After evaluation by two reviewers, there are a number of points that should be addressed before a recommendation is possible.

The most important issue, perceived somewhat differently by the two reviewers, is the lack of highly significant effect when the pathogenicity of *Z. tritici* isolates is compared at the intra-annual scale ( $p=0.087$ ), whereas this effect is emphasized and deeply discussed and interpreted (overinterpreted?).

While the  $p=0.05$  significance threshold can be considered somewhat arbitrary, it is widely accepted in the scientific community. This effect should therefore be interpreted as a trend rather than a definitively established effect and its interpretation in the Discussion should be taken with more caution and be given less importance. You can for example argue that the trend observed during a single year results from differential selection effects that would have needed to be maintained during several years to reveal more significant effects.

Please consider also the additional reviewers' comments.

## Reviewed by anonymous reviewer 1, 02 September 2017

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## Reviewed by **Benoit Moury**, 04 August 2017

The manuscript « Trade-off between intra- and interannual scales in the evolution of aggressiveness in a local plant pathogen population » by Suffert et al. shows an analysis of the evolution of aggressiveness of a fungal pathogen, *Zymoseptoria tritici*, in a wheat cultivar with a medium resistance level. To do so, *Z. tritici* isolates were collected in field plots and their aggressiveness evaluated in controlled laboratory conditions on the same wheat cultivar plus another one representing an allopatric host.

The evolution of quantitative life history traits of plant parasites exposed to host plants which themselves harbor quantitative resistance factors is poorly understood and poorly studied. Notably, the speed at which parasite adaptation takes place in these conditions has rarely been determined. The important advance of Suffert et al. is to help determine the appropriate timescale to measure the gain of adaptation of the parasite. Indeed, in this study, Suffert et al. compared *Z. tritici* isolates (i) at the annual scale, i.e. before and after they had been exposed to the host plants during one growing season only and (ii) at the interannual scale, i.e. before and after six years of exposure. Importantly, if comparisons at the intra- and inter-annual scales lead to opposite conclusions about the capacity of the parasite to adapt to its host, then multiple timescales should be more systematically taken into account for such studies and particular caution should be taken in interpreting data focusing on only one particular timescale. Indeed, considering the « local » host cultivar on which the parasite most probably evolved, a gain of adaptation (shorter latent period, though the effect was marginal with  $p=0.087$ ) was observed at the intra-annual scale, whereas no adaptation change was observed at the inter-annual scale.

The experiments in Suffert et al. are well designed and described. My only regret is that the populations Ci-2009 and Cf-2010, compared to study adaptation at the intra-annual scale, were not tested on the « allopatric » cultivar Apache. This may have allowed to check if adaptation to the allopatric host could also occur during this timeframe. In addition, I would have liked some more details about the representativity about the 15 isolates in each population, if such data exist. Can we exclude any strong bias between the 15 isolates and the overall epidemic parasite population? This is particularly true for populations Cf-2010, Ai-2009 and Af-2015 for which we have no details about sampling. Maybe the information is available in other publications by the same group, but it would be worth providing brief elements here.

I have several more specific points that may help clarify the manuscript and for which I would like a revision.

### **Introduction.**

-page 2, column 1, « Alternatively, selection may be negligible relative to other antagonistic selective forces (gene flow...». As the word 'selection/selective' is in the two parts of the sentence, the idea is not clear. Moreover, I consider gene flow and selection to be quite distinct evolutionary forces.

### **Materials and Methods.**

-For lesion size, I did not get which variable was analyzed (size at final date, all dates, AUDPC...). Can you be more precise ?

-Which software was used for data analyses ?

### **Results.**

-Table 1 : Can you indicate which r values are significant ?

-page 7, column 1 : « ...consistent with of the generally... » -> replace with « ...consistent with the generally ... »

-Figure 5 : Can you compare statistically the two distributions ?

-page 7, column 2 : « ...with an early attack following moderate winter... »-> replace with « ...with an early attack followed by moderate winter... ».

-Lesion growth curves that did not fit with the Gompertz curves were excluded from analysis. However, the Gompertz parameters were used only to determine the latent period. You could have used these data for the analysis of the lesion size. Does it affect the results ?

-page 8, column 1 : I would prefer « isolate - cultivar combination » to « isolate x cultivar interaction » here.

### **Discussion.**

-page 10, column 2 : Is it two pairs or one pair of *Z. tritici* populations here ? I understand that the cultivar effect could be tested only with the Ci-2009 and Cf-2010 populations.

-page 10, column 2 to page 11, column 1 : I do not completely agree with the interpretation of the data as maladaptation to the allopatric host, Apache. I find that it depends on the point of view and the statement may be modulated. Considering the latent period, it is true that populations Ai-2009 and Af-2015 perform better on the sympatric than on the allopatric host. However, on the allopatric host, the Af-2015 population induces larger lesions than Ai-2009, hence, in my vision, it gained adaptation to the allopatric host along the six years of exposure to the sympatric host.

-page 11, column 1 : « A host shift alters the environment... » : I did not understand that sentence.

-page 11, column 1 : « ...at least partly due to evolutionary forces (as opposed to chance)... »->replace with « ...at least partly due to deterministic evolutionary forces (as opposed to chance)... ».

-page 11, column 2 : « ... the effects of selection are much smaller than those of diversity... » : I do not understand the idea here.

-page 11 column 2 : « Phenotyping isolates on adult plants, ... (Morais et al., 2016a) » : I do not understand how such phenotyping allows to draw that conclusion.

-page 12, column 1 : I do not really understand how the local host maladaptation (that may be discussed as mentioned above) and the temporal continuity of pathogen pressure « demonstrate the robustness of this analysis ». Could you explain more ?

-page 12, column 1 : « The trade-off between the capacity to overcome... » : among the traits compared, one belongs to the parasite and the other to the host ; thus I do not see any trade-off here.