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Towards an integrated scenario to understand evolutionary patterns in A. thaliana

Xavier Picó *based on peer reviews by* ***Rafa Rubio de Casas*** *and* ***Xavier Picó***

Glander S, He F, Schmitz G, Witten A, Telschow A, de Meaux J (2017) Assortment of flowering time and defense alleles in natural Arabidopsis thaliana populations suggests co-evolution between defense and vegetative lifespan strategies. Missing preprint_server, ver. Missing article_version, peer-reviewed and recommended by Peer Community in Evolutionary Biology. 10.1101/131136

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Nobody can ignore that a full understanding of evolution requires an integrated approach from both conceptual and methodological viewpoints. Although some life-history traits, e.g. flowering time, have long been receiving more attention than others, in many cases because the former are more workable than the latter, we must acknowledge that our comprehension about how evolution works is strongly biased and limited. In the *Arabidopsis* community, such an integration is making good progress as an increasing number of research groups worldwide are changing the way in which evolution is put to the test. This manuscript [1] is a good example of that as the authors raise an important issue in evolutionary biology by combining gene expression and flowering time data from different sources. In particular, the authors explore how variation in flowering time, which determines lifespan, and host immunity defenses co-vary, which is interpreted in terms of co-evolution between the two traits. Interestingly, the authors go beyond that pattern by separating lifespan-dependent from lifespan–independent defense genes, and by showing that defense genes with variants known to impact fitness in the field are among the genes whose expression co-varies most strongly with flowering time. Finally, these results are supported by a simple mathematical model indicating that such a relationship can also be expected theoretically. Overall, the readers will find many conceptual and methodological elements of interest in this manuscript. The idea that evolution is better understood under the scope of life history variation is really exciting and challenging, and in my opinion on the right track for disentangling the inherent complexities of evolutionary research. However, only when we face complexity, we also face its costs and burdens. In this particular case, the well-known co-variation between seed dormancy and flowering time is a missing piece, as well as the identification of (variation in) putative selective pressures accounting for the co-evolution between defense mechanisms and life history (seed dormancy vs. flowering time) along environmental gradients. More intellectual, technical and methodological challenges that with no doubt are totally worth it.

References:

[1] Glander S, He F, Schmitz G, Witten A, Telschow A, de Meaux J. 2017. Assortment of flowering time and defense alleles in natural *Arabidopsis thaliana* populations suggests co-evolution between defense and vegetative lifespan strategies. bioRxiv ver.1 of June 19, 2017. doi: [10.1101/131136](https://doi.org/10.1101/131136)

Reviews

Evaluation round #1

Reviewed by **Xavier Picó**, 06 July 2017

The manuscript entitled ”Assortment of flowering time and defense alleles in natural Arabidopsis thaliana populations suggests co-evolution between defense and vegetative lifespan strategies” by Glander, He, Schmitz, Witten, Telschow, and de Meaux, addresses an extremely challenging and interesting question in plant biology. The authors seek to understand how plants manage to complete their life cycle whilst coping with pathogens activating genetic defense mechanisms during the vegetative growth period. To this end, the authors make use of various tools, such a model to explore how changes in life history can alter the costs and benefits of host defense systems, readily available data sets from collections of natural accessions including flowering time and genome-wide expression profiles, and experimental data to evaluate the correlation between gene expression and flowering time using the well-known Bur-0 x Col-0 Recombinant Inbred Lines. Overall, the authors are able to provide solid evidence that the higher expression of defense genes and the increase of lifespan duration in A. thaliana have been shaped by natural selection. With no doubt, this work widens our understanding on plant evolution. Below, I go through some issues and concerns with the aim to improve this manuscript.

Given that this manuscript deals with flowering time as a proxy for lifespan, it would be useful to see frequency distributions for flowering time for the different sets of accessions used in this study. I also suggest a panel with the geographical position of accessions (the 138 Swedish accessions from Sasaki et al. 2015, and the 144 accessions from Schmitz et al. 2013) along with the frequency distributions for flowering time for these two accessions plus that for the RILs.

In addition and related to the previous point, it seems that the authors work with accessions that did not require vernalization for flowering. It makes sense as a vernalization treatment prevents to quantify lifespan properly. However, I want to draw the authors' attention to the fact that vernalization is a very common requirement for flowering in natural environments, and thus an important aspect of A. thaliana's biology. I missed some discussion about this important fact just to better frame the conclusions of the work. In my opinion it's not a big deal as vernalization in natural conditions can start quite early after germination. In the case of high altitude populations in the Pyrenees, where spring germination events in late winter or early spring are common and crucial for population persistence, temperatures can be very low during germination and recruitment. We know that plants do not require freezing temperatures but cold ones to get vernalized. Normally, genotypes from high altitude environments require a vernalization requirement for flowering. In the greenhouse, these genotypes can take up to 250 days of vegetative growth for flowering, but in the field they may show short lifespans if they emerge in late winter. This may appear paradoxical, but contrasting lab data with field data is always problematic as the sources of variation are very different. Although this point is partially addressed in this manuscript, in my opinion it requires more attention.

Another important aspect that may also enrich this manuscript is the current knowledge on the response of A. thaliana to biotic and abiotic stresses. Genetic defense mechanisms have been evolving along with the biotic and abiotic selective pressures affecting plants. Two empirical studies by Davila-Olivas et al. on the plant's response to different stresses have recently been published providing valuable insight into this important aspect of A. thaliana's evolutionary history (see New Phytologist, 2017, 213: 838-851, doi: 10.1111/nph.14165; Molecular Ecology, 2017, 26: 2959-2977, doi: 10.1111/mec.14100). These two studies show how life history may explain the susceptibility of A. thaliana to different biotic and abiotic stresses, which overall is quite relevant in the context of this manuscript. I'm quite sure that the authors will find interesting findings to enrich their manuscript.

In general terms, I totally agree with the major take-home messages of this study. However, in some parts of the text the authors refer to the effect of past epidemics on the current defense mechanisms. In other words, they try to build a hypothetical scenario on the causes of what they are studying. I find this a bit confusing because it is really difficult to proof it. In my opinion and based on my observations and field data, A. thaliana strongly adapts to its environment by modifying germination time, flowering time, and the correlation between the two traits. Large-scale climatic variation shapes up life history in A. thaliana and in many other terrestrial organisms. Pathogens and insects are less global but much more local, so my hypothesis is that local populations become adapted to biotic stresses after adjusting life history major events to the abiotic environment. It would be important to pose a more specific hypothesis about how defense mechanisms and life history co-evolved in A. thaliana.

Finally, I ignore whether the authors possess data on seed dormancy or germination behavior for the three sets of accessions used in their study. To date, flowering time variation can no longer be understood without seed dormancy variation. It is widely accepted that the two traits are closely related to each other and that they strongly co-evolve. In a context of developmental niche construction, we know that changes in the timing of life-stage transitions determine the environment experienced subsequently, which in turn affects subsequent phenotypes (see the vast work by K. Donohue on this exciting topic). Thus, it would be very interesting to take seed dormancy into account in this study as the co-evolution between flowering time and defense mechanisms cannot exclude seed dormancy and germination timing. As a matter of fact, we are talking about three players in this evolutionary scenario.

Reviewed by **Rafa Rubio de Casas**, 07 July 2017

Comments to Glander et al. This paper is convincing and well conducted analysis of the connection between life-span, as measured by flowering time (FT) in Arabidopsis thaliana and the expression of defence genes. The authors put forward their working hypotheses with the help off a simple mathematical model and base their conclusions on abundant data and well-designed experiments. I sincerely recommend this preprint, although I have few suggestions that hopefully will be helpful. My first suggestion would be to re-work the link between the mathematical model and the rest of the manuscript. Currently, the model is somewhat of a non-sequitur. I think it needs a little more thought and more integration with the rest of the ms. It seems like a clever formalisation of the association between lifespan and defence costs. However, some of the assumptions are unclear. For instance, why is the relationship between d and L linear? Aren't pathogens more likely to attack certain life stages than others? Actually, results presented later in the manuscript show age-dependent gene expression, so maybe d should not vary constantly with age... Furthermore, the amount of data and results are conclusive and convincing enough. The value added by the mathematical model is small, if any. I think that formalising the conceptual model mathematically can be a powerful and elegant improvement relative to just using verbal explanations, but in this case the connection between the mathematical and empirical sides of the manuscript is tenuous. Maybe the authors could reinforce it, but on the other hand, maybe they just don't need to and they can just forego the mathematical model altogether. Reworking Figure 1 could be one way to make the connection more straightforward. This figure would be more useful if it displayed a clear graphical prediction of the relationship between flowering time and defence. A plot showing the relationship between only those two variables could be included as an. A figure showing clearly the theoretical expectations regarding a positive correlation between life-span and defence investment would present the main hypothesis at a glance. There is also some room for clarification in the bulk-segregant analysis, which I find one of the most interesting components of the ms. It is an elegant and powerful way of controlling for pleiotropy. However, I think that the concept (i.e., pleiotropy between defence and flowering time) should be presented earlier, likely in connection with the theoretical expectation of a link between the two traits. Also, the interpretation of the molecular results of this analysis needs some further clarification. For instance, how were non-FT-controlled genes identified in this experiment? (in page 6 “Defense genes, whose expression was not controlled by flowering time,…”). That seems to be a crucial result and needs to be well explained. More minorly, the ms seems to require some careful proofreading before sending it out for publication. There are some small mistakes & typos throughout. For instance, there is only one paper of Burghardt et al in the bibliography, although Burghardt 2015a and 1015b are referenced in the text. Also, the figure legends need some editing (what is the meaning of the arrows in Fig. 4?; why is there a “what is group A?” call in Supp. Figure 1?).