Peer Community In
Evolutionary Biology

When ecology meets genetics: Towards an integrated understanding of mating system transitions and diversity

Sylvain Billiard and *Henrique Teotonio* *based on peer reviews by* *Yaniv Brandvain*, *Henrique Teotonio* *and 1 anonymous reviewer*

In the 19th century, C. Darwin and F. Delpino engaged in a debate about the success of species with different reproduction modes, with the later favouring the idea that monoecious plants capable of autonomous selfing could spread more easily than dioecious plants (or self-incompatible hermaphroditic plants) if cross-pollination opportunities were limited [1]. Since then, debate has never faded about how natural selection is responsible for transitions to selfing and can explain the diversity and distribution of reproduction modes we observe in the natural world [2, 3]. Explanations for mating systems diversity, and transitions to selfing in particular, generally fall into two categories: either genetic or ecological. On the genetic side, many theoretical works showed a critical role for mutation load and inbreeding depression, transmission advantage and reproductive assurance in the evolution of selfing, e.g. [4]. Many experimental works were conducted to test theoretical hypotheses and predictions, especially regarding the magnitude of inbreeding depression; see [5] for a review. Ecologically, the presence of selfing populations is usually correlated with fragmented and harsh habitats, on the periphery of ancestral outcrossing populations. The cause of this distribution could be that selfers are better dispersers and colonizers than outcrossers, or variations in other life-history traits [6]. Yet, few experiments were run to assess whether selfing species or populations have effectively different ecological characteristics, and even scarcer are experiments evaluating both the roles of mutational load and life-history traits evolution. This is the aim of the present study by X. Yang et al [7]. The study of Yang et al [7], together with that of Petrone Mendoza et al. [8], supervised by S. Glémin and M. Lascoux, is probably one of the first to conduct experiments where the competitive abilities are compared between and within species. Using 4 species of the Capsella genus, annual

plants from the mustard family, they tested the theoretical predictions that i) the transition from outcrossing to selfing resulted in reduced competitive ability at higher densities, because of the accumulation of deleterious mutations and/or the evolution of life-history traits in an open habitat and a colonization/dispersal trade-off; ii) that reduced competitive ability of selfers should be less pronounced in polyploid then diploid species because the effect of partially recessive deleterious mutations would be buffered; and iii) that competitive ability of selfers should decline with historical range expansion because of the expansion load [9]. Of the 4 Capsella species studied, only one of them, presumably the ancestral, is a diploid outcrosser with a small distribution but large population sizes. The three other species are selfers, two diploids with independent histories of transitions from outcrossing, and another, tetraploid, resulting from a recent hybridization between one of the diploid selfer and the diploid outcrossing ancestor. Many accessions from each species were sampled and individuals assayed for their competitive ability against a tester species or alone, for vegetative and re-productive traits. The measured vegetative traits (rosette surface at two stages, growth rate and flowering probability) showed no differentiation between selfers and outcrossers. To the contrary, reproductive traits (number of flowers) followed theoretical predictions: selfing species are more sensitive to competition than the outcrossing species, with polyploid selfing species being intermediate between the diploid selfers and the diploid outcrosser, and within the tetraploid selfing species (where sampling was quite significant across a large geographical range) sensitivity to competition increased with range expansion. The study of Yang et al. [7] suffers from several limitations, such that alternative explanations cannot be discarded in the absence of further experimental data. They nonetheless provide the reader with a nice discussion and prospects on how to untwine the causes and the consequences of transitions to selfing. Their study also brings up to date questions about the joint evolution of mating system and life-history traits, which needs a renewed interest from an empirical and theoretical point of view. The results of Yang et al. raise for instance the question of whether it is indeed expected that only reproductive traits, and not vegetative traits, should evolve with the transition to selfing. The recommandation and evaluation of this paper have been made in collaboration with Thomas Lesaffre.

References:

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[6] Munoz, F., Violle, C. & Cheptou, P.-O. (2016). CSR ecological strategies and plant mating systems: outcrossing increases with competitiveness but stress-tolerance is related to mixed mating. Oikos, 125(9), 1296-1303. doi: [10.1111/oik.02328](https://dx.doi.org/10.1111/oik.02328)

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Reviews

Evaluation round #2

Authors' reply, 24 May 2018

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Decision by Henrique Teotonio, posted 24 May 2018

recomment but with revisions

Dear Sylvain,

I've now received one review of the revised manuscript you sent us, and I'm happy to write that I will recommend it for publication. This said, there are a few issues that you could address in a last round of revisions to strengthen the manuscript.

The last point of the reviewer is pertinent. It could be made clearer in the discussion that vegetative traits may be involved in direct competition between individuals, even if you have not measured them, while reproductive traits may be involved in reproductive assurance and/or colonization ability. If you could show that rosette surface is a fitness component, wouldn't the difference in the responses to your treatments be indicative that there is a trade-off between colonization and competition?

On page 11, at least in the version I have, the equation for the competitive index is missing. And in the last sentence of the paragraph you use the term "accession", shouldn't it be "species"?

Page 14, the genetic diversity in China is of 0.0015, right?

On page 16, you mention one Figure 5, typo?

I am not entirely sure that the statistical analyses you perform are well explained. First, I feel that some of the models are likely prone to collinearity. For example, in the model presented in table 3, I don't understand the rationale to include "rosette surface at t2" and "rosette" as separate factors; "growth rate" would be more appropriate? Can you test for collinearity even if in the end you don't present it in the manuscript? Stating only that you prevent over parameterization by dropping factors and their interactions does not seem to be sufficient. Second, I think that the analysis and presentation would be much clearer and simple if you use the competitive index as the dependent variable throughout. At several places you write that a particular factor "explains" or "causes" differences in the competitive index, but in reality you never test it. A figure with the competitive index estimates (including confidence or credible intervals) would be nice. Third, the models testing for the effects of genetic diversity should include it as a covariate and not as a fixed factor. The main reason for this is that you did not manipulate genetic diversity levels and thus cannot test for interactions

between what you think are the independent variables. It's not clear to me if area shouldn't be tested as a covariate or as a fixed factor. The model of Table 3 is also confusing in this regard.

One last comment is that I find that you easily equate levels of genetic diversity with the presence of deleterious genetic loads, which in turn will result in the short-term maintenance of selfing. Alternative and mutually-exclusive explanations are that selfing populations are initially better able to purge ancestral inbreeding depression, and thus better survive potential bottlenecks during range expansion than outcrossing populations, or because they actually have increased additive genetic variance for fitness traits, due to expression of dominance and epistasis, and thus respond faster to selection in novel environments. The observed levels of genetic diversity do not contradict these ideas. You suggest at one point in the discussion that measuring inbreeding depression in these populations would be important but I'm not sure that the reader will really appreciate these alternative explanations.

Finally, in the code of conduct, it is specified that:

-Data for preprints must be available to readers after recommendation, in the preprint or through deposition in an open data repository, such as Zenodo, Dryad or institutional repositories, for example.

-Details of the quantitative analyses (e.g. data treatment and statistical scripts in R, bioinformatic pipeline scripts, etc.) in the recommended preprints must be available to readers in the text or as appendices or supplementary materials, for example.

-Details of the experimental procedures in the recommended preprints must be available to readers.

Please, ensure that your preprint is in line with these requirements

With my best wishes, Henrique

Reviewed by anonymous reviewer 1, 06 April 2018

Please find our review in the attached file.

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Evaluation round #1

DOI or URL of the preprint: **10.1101/214866**
Version of the preprint: 1

Authors' reply, 05 April 2018

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Decision by **Henrique Teotonio**, posted 05 April 2018

Revise

Please see my letter

Reviewed by **Henrique Teotonio**, 13 November 2017

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Reviewed by anonymous reviewer 1, 20 November 2017

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Review of "Competitive ability of a tetraploid species across its expansion range and comparison withers sister species"

In this paper Yang et al compare fitness proxies of outcropping and diploid and tetraploid selfing capsella species with an without a competitor. The authors find that diploid selfing species have the greatest fitness reduction upon competition with an aster species. The authors find that both diploid selfing species have a proportionately greater reduction in fitness upon competition than the polyploids selfing species and the polyploid seller, which itself has a proportionally greater reduction in fitness upon competition than does the outcrosser. These results are interesting. That said I have numerous comments that would improve the paper

THE TITLE. This paper is written to about much more than the polyploid (C. bp), but this species is the focus of the title. I suggest the authors change this. Perhaps "Mating system, ploidy and range expansion shape the competitive ability of four Capsella species" would be more appropriate.

THE FIGURES.'slope-o-graphs' would be a better way to present all of the data, as opposed to paired box and whisker plots facetted by species (or geography). Additionally the Ic bar plots do not add too much (especially once the data are better presented) and could be removed.

Ic - I realize this has been presented in a separate manuscript, but ratios like this retouch for me to follow / comprehend for numerous reasons. First of all, they can be difficult to interoperate bc its not clear if results are driven by the numerator or denominator (e.g. rosette area in chinese c. bp). Second, such ratios are more naturally interpreted as logs, so i suggest log transformation.

STATS - On the whole the stats are well described and well justified. However, (as above) I am confused by the statistical approach taken to analyze Ic. It seems like this can be interpreted roughly as the interaction species X competition interaction term in the linear model (except as a ratio rather than a linear effect). As such it seems like this should be a post-hoc test rather than an independent one. Also I worry if these ratio data are normal (see above). That said, these are somewhat minor gripes.

DIFFERENCES IN SURVIVORSHIP - On page 10 we are told 'The flower number distribution was bimodal with a mode at 0 and another around 1000 (see results). Thus it was analysed in two steps. First, we analysed the proportion of flowering plants with a binomial model and a logit link using the glmer function of the R package lme4 (Bates et al. 2015). Dead plants were included in the non-flowering category. Second, we excluded plants that did not flower and analysed flower number with a negative binomial model and a log link with the glmmadmb function of the glmmADMB package (Fournier et al. 2012; Skaug et al. 2013).' — However, I did not see this bimodal distribution presented, and did not see any results concerning survivorship. Did I somehow miss this?

DIVERSITY's IMPACT ON THE RESPONSE TO COMPETITION - The authors find a strong positive relationship between sequence diversity and Ic across C. bp. However, as the authors' show this effect can be fully explained by geography, Because these pi values are not independent, I do not think this is a robust result, and I think it should be omitted from the manuscript. In it's place should be a section of the discussion noting that at the population level (n=3) the rank order of population diversity was the same as the rank order of Ic. This would be a more responsible and correct presentation of the results.

SCOPE OF EXPLANATION / RELEVANCE The results presented in this manuscript are exciting, and suggest an interesting potential effect of mating system, polyploidy and geographic position on how competition impacts fitness. However this is a very small sample size (4 species), so it might be best to emphasize that this suggests a pattern but many more experiments in other taxa are required.

MECHANISM The authors propose alternative hypotheses to explain these patterns (basically adaptation vs drift). They do a responsible job of not committing to one of these alternatives bc the data do not currently allow it. However, it seems like a set of crossing experiments could untangle these. It would be nice if the authors discussed how future experiments could differentiate these hypotheses.

MINOR COMMENT On page 16, the authors state that "selection is expected to be softer when interspecific competition is low." I think the authors are making a mis-statement and that they meant to say "selection is

expected to be LESS SEVERE when interspecific competition is low." I suggest staying away from the phrase 'soft selection' because this could be confused for its more technical meaning (which I don't think the authors intend). In fact, according to the technical term, I think that selection is probably best considered 'hard' in the absence of competitors and 'soft' in their absence.