Peer Community In
Evolutionary Biology

Evolution of selfing & lifespan 2.0

Thomas Bataillon *based on peer reviews by 2 anonymous reviewers*

Flowering plants display a staggering diversity of both mating systems and life histories, ranging from almost exclusively selfers to obligate outcrossers, very short-lived annual herbs to super long lived trees. One pervasive pattern that has attracted considerable attention is the tight correlation that is found between mating systems and lifespan [1]. Until recently, theoretical explanations for these patterns have relied on static models exploring the consequences of several non-mutually exclusive important process: levels of inbreeding depression and ability to successfully were center stage. This make sense: successful colonization after long-distance dispersal is far more likely to happen for self-compatible than for self-incompatible individuals in a sexually reproducing species. Furthermore, inbreeding depression (essentially a genetically driven phenomenon) and reproductive insurance are expected to shape the evolution of both mating system and lifespan. But modelling jointly several processes and how their interplay to shape the evolution of a trait is challenging enough so models for the evolution of mating system tend invariably – for mathematical convenience and tractability – to fix lifespan [2]. However, comparative analysis of between species variations that map traits transitions among sister species in phylogenetic trees reveals a pervasive pattern: frequent transitions from a state outcrossing perennial to selfing annuals. This beg the question: is one transition triggering the other and if so, what comes first or are these transitions happening together? In this work, Lesaffre and Billiard use a very sophisticated machinery developed by Kirkpatrick et al. [3] and consider a general class of so-called modifiers models [4]. They study jointly the evolution of life span and mating system. They do so by using models where different life stages are tracked with life stage having some (fixed for once) amount of inbreeding depression. Their paper is technically demanding, mixing analytics and computer simulations, and along the way generates several important findings that are expected to stimulate further empirical and theoretical studies: (1) pure selfing versus pure outcrossing is the expected stable evolutionary outcomes (despite observation that mixed mating systems can be regularly met in nature), (2) increasing life-span drastically reduces the scope for the evolution of selfing, conversely (3) transition to selfing will also select for shorter life span as a way to mitigate the cumulative effects of inbreeding depression on adult life stages. As usual there is room for future work,

in particular the authors' model assumes fixed inbreeding depression in the different life stages and this highlights the need for models that explore how inbreeding depression, a pivotal quantity in these models, can itself be molded by both mating system and lifespan. A third-generation of models should be "soon" on the way!

References:

[1] Grossenbacher D, Briscoe Runquist R, Goldberg EE, and Brandvain Y. (2015) Geographic range size is predicted by plant mating system. Ecology Letters 18, 706–713. doi: [10.1111/ele.12449](https://dx.doi.org/10.1111/ele.12449)

[2] Morgan MT, Schoen DJ, and Bataillon T. (1997) The evolution of self-fertilization in perennials. The American Naturalist 150, 618–638. doi: [10.1086/286085](https://dx.doi.org/10.1086/286085)

[3] Kirkpatrick M, Johnson T, and Barton N. (2002) General models of multilocus evolution. Genetics 161, 1727–1750.

[4] Lesaffre, T, and Billiard S. (2019) The joint evolution of lifespan and self-fertilisation. bioRxiv, 420877, ver. 3 peer-reviewed and recommended by PCI Evol Biol. doi: [10.1101/420877](https://dx.doi.org/10.1101/420877)

Reviews

Evaluation round #2

DOI or URL of the preprint: **10.1101/420877**
Version of the preprint: 2

Authors' reply, 18 March 2019

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Decision by **Thomas Bataillon**, posted 25 February 2019

Revisions needed for your MS "The joint evolution of lifespan and self-fertilisation"

Dear Thomas & Sylvain First apologies for the very lengthy review process on that round!

Please find enclosed a last set of comments by the two anonymous reviewers.

Basically one of the reviewer is "content" but the second reviewer made a thorough reading of your revised version and flags a number of issues where possibly minor but important clarifications are still needed. He also make some suggestions for minor text reorganisation that are not compulsory per se but well worth considering

I am trusting that these last outstanding issues can be rapidly resolved within a week or two and I will be happy to recommend this paper provided that the revisions and clarifications suggested are implemented (no further review round will be needed).

While you prepare this last needed revisions, I will meanwhile draft my recommendation text.

Thanks again for submitting this interesting piece of theory for recommendation to PCI Evol Biology I look forward to your last and final revised version and to recommend your work within PCI Evol Biology

Kind regards

Thomas

Reviewed by anonymous reviewer 3, 21 December 2018

This manuscript is much improved. I appreciate all and is as close to being the best version of the paper that could be written, given the major assumptions and caveats that the authors are well aware of. It is still unclear to me if this result is

(A) a simple artifact of the lack of an apple-to-apples comparison between life history, as lifetime inbreeding depression is not held constant or (B) An important contribution pointing out that lifetime inbreeding depression will vary by lifespan and this has important consequences.

While an apples to apples comparison would strengthen the paper, it's unclear if that is realistic anyways.

Ultimately the answer to my concern will be settled by the paper's reception,

Reviewed by anonymous reviewer 2, 21 December 2018

In this revision, Lesaffre and Billard have updated their manuscript by adding new figures to clarify their results; elucidating the mathematical derivations; and include new results on the effect of inbreeding depression if it affects fecundity. The manuscript has been improved as a result but still needs further revising before it can be fully recommended.

(1) Outline of the methods. The introduction of the 'Model Outline' section needs some editing, as it combines mathematical results with simulation methods in an inconsistent manner, making it hard to follow. I propose streamlining it, so it first gives an overview of the basic model; then a description of the simulation/numerical methods, before presenting mathematical results from section 2.1 onwards.

Some specific points: • The methods and results that include inbreeding depression based on fecundity (e.g. P6 L103–104, section 2.3.2) seem oddly placed since they are not included in the basic model. I propose moving these results, along with a short description on how the simulation was changed, to a separate appendix. • The paragraph on the effects of inbreeding depression (P6 L105-112), and the results on the proportion of selfed individuals (P6–7 L120–127), should be moved to section 2.1 so all the mathematical results, and their interpretation, are placed together.

(2) Figures. I'd like to thank the authors for including the new Figures 2–4, along with the simulation results. Together they greatly improve the manuscript. That said, they could still do with some refinement: • Figure 2: Each panel is quite hard to read since both the arrows and the simulation points are very small. In addition, the text on P12 L241–246 that describe the figures themselves should be added to the caption for Figure 2. Finally, it seems that the phase trajectories deviate from the theoretical expectations for high selfing values in the first two panels; why is that? • Figure 3: Here too the simulation points could be made bigger, and the text on P13 L260–264 also seems like it should be added to the caption. There does not also seem to be a discussion on the meaning of these results. • Figure 4: The caption for each subfigure should be changed, as it appears to suggest that the *ratio* of δ_j/δ_f is the parameter that is being changed. • Finally, please consider adding the parameter name to the axes for all figures, and not just the symbol.

(3) Mathematical derivations. I'd also like to thank the authors for updating Appendix II, however I have to admit that I still cannot follow some of their derivations. In particular, while $D_{m,m}$ is now defined for juveniles, it is unclear how A18 follows from A17. It seems that if there's a $\delta_{m,m}$ term, then X_{jm} is somehow related to X_m but it is not made clear. Could the author clarify this point, and double–check the rest of the appendix to improve the clarity of the derivations where necessary?

Some small suggestions for improving the main text: • P3 L57: Write "on *the* one hand". • P3 L60: Replace "was only" with "has only been". Similarly, for P4 L62, replace "was never tacked" with "has never been tackled". • P9 L191: Replace 'get' with 'are'. • P9 L194: Should this be 'differentiating' instead of 'deriving'? • P10 L224:

Write 'there are' instead of 'there is'. • P15 L273: Write 'in both cases' • P15–16 L275–276: "thereby diminishing the proportion of selfed individuals in the population" repeats what was previously written, so should be deleted.

Evaluation round #1

Authors' reply, 18 December 2018

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Decision by **Thomas Bataillon**, posted 29 October 2018

Revisions needed for your MS "The joint evolution of lifespan and self-fertilisation"

I am acting as recommender for PCI Evol Biol for your manuscript "The joint evolution of lifespan and self-fertilisation" Authors: Thomas Lesaffre, Sylvain Billiard **https://doi.org/10.1101/420877** version 1 - **https://www.biorxiv.org/content/early/2018/09/18/420877for** recommendation at PCI Evol Biol.

Your manuscript has now been evaluated by two referees. Both have expertise in theoretical population genetics and an interest for mating system evolution. Both reviewers (see detailed reviews) and myself agree that your manuscript has potential to be an interesting contribution that is suitable for being recommended at PCI Evolutionary Biology. But we all feel that before this can happens, fairly extensive revisions should be made.

Here is a synthetic list of the major points that need imperatively to be addressed:

* Reviewer 1 has a number of fairly precise requests (labelled 1 and 2 in the review). These have to do with the presentation of the main results as well as request for clarifying the derivation of the theory results.

* Reviewer 2 has a series of more general comments that are worth considering while revising your manuscript. One important one (labelled comment 2) is how to compare the propensity to evolve selfing while "holding lifetime levels of inbreeding depression constant". I think that is an important point that together with the points raised by reviewer 1 merits to be addressed in quite a bit of depth.

* Point 4 should be considered at least in the discussion.

* Point 5 is relatively minor but the rev2 has a point regarding what is empirically known on the genetic basis of inbreeding depression.

I very much hope that you can revise your MS to take into account these points.

Best Regards Thomas Bataillon

Reviewed by anonymous reviewer 2, 19 September 2018

Self-fertilising organisms are generally short-lived in nature, while outcrossers are likelier to be long-lived. Previous theoretical research has investigated why this arises, while assuming a fixed lifespan. Here, selfing is disadvantageous in perennials due to the reduced need for reproductive assurance, and the unmasking of inbreeding depression. In this paper Lesaffre and Billiard use multi-locus models to investigate mating systems evolution if lifespan itself can jointly evolve with lifespan. Under this scenario, selfing causes evolution of shorter lifespans in order to maximise reproduction; yet this phenomenon can exacerbate the impact of inbreeding depression, so selfing is less likely to survive in the long-term.

The novel mathematical arguments are nicely laid out, outlining how the joint evolution of mating systems with other phenomena (in this case, lifespan) can alter expectations of how reproductive strategies can be

maintained. The theory seems to be generally correct. That said, I feel a bit more work needs to be done in order to fully clarify and support the main claims in the manuscript.

(1) Clearer presentation of main results The most important finding is that the joint evolution of mating system and lifespan should further select against self-fertilisation compared to a scenario where lifespan is fixed. Yet it's hard to understand this result from Figure 2, which only outlines the steady-state lifespan for different values of inbreeding depression. There is not a figure to show, for example, how the same ID parameters affect the steady-state mating system when lifespan is fixed.

At the very least, this figure needs updating (or a new figure added) to fully demonstrate how the steady-state mating system is affected by evolving lifespan. Such a figure, as well as Figure 2 if it remains, should also include the exact numerical results so the reader is confident that the approximations accurately capture the behaviour of the system.

Figure 2 is also hard to read: the text on each plot is very small and not easy to read. The font sizes should be made bigger. In the legend, it states that "The solid line corresponds to the threshold inbreeding depression condition below which selfing evolves". I presume that the 'threshold inbreeding depression' refers to thresholds for both juvenile and adult inbreeding depression? If so this point should be made clearer.

(2) Further details of the mathematical derivations. The mathematical arguments seem broadly correct, but I found at least one possible error, and a few cases where more information could be provided to aid mathematical readers in understanding the derivations used.

• For the equilibrium proportion of selfed individuals Θ^* (Equation 1 and A5), I obtain a different solution; I believe the denominator should be $\square$ $(1 – \square j)(1 – S_0(e)) + (1 – \square)$ $(1 – S_0(e)$ $(1 – \square a))$. I'm unsure if this error is solely typographical, or whether it permeates throughout the rest of their derivations. I suspect the former, since Equation A8 holds for $S_0(e) = 0$ if the denominator I obtained is used. The authors should carefully check their other equations for errors. • It would be good to mention somewhere that $E(\square m) = 0$. • It's unclear how the linkage disequilibrium measurements across life stages (i.e. A17 and A23) are obtained using the multi-locus framework. Does it require defining and working with stage-specific indicator variables (e.g. $\square jm = Xjm – pjm$, and similar for the maternal chromosome)? • How is Dm,m obtained? *It seems that one invokes 'Quasi-linkage equilibrium' assumptions; that is the selective forces ($\square$ and pm) are weak so Dm,m = D'm,m = Dm,m*. However, I could not recover A25 when using these assumptions. Please provide further information on this derivation. • Does the derivation of A26 require D*m,m (A25)?

(3) Minor issues (P = page number, L = line number) • P1, abstract: 'for instance' is not needed here and could be deleted. • P4 L73: 'anterior' does not make sense in this context. Best to use 'previous' instead. • P6 L109: 'overlapping generations' reads better than 'generations overlap'. • P6 L115: 'no approximations' instead of 'no approximation made'. • P7 L126: Would be good to point out that $\square \ll 1$. • P7 Eq 2: It would be nice to briefly explain why this function form of $S_0(e)$ is used (I presume because it's rather flexible?). • P8 L158: 'In addition' would be a better phrase to use than 'Besides'. • P15 L316: Please delete the ellipsis (...).

Reviewed by anonymous reviewer 3, 19 September 2018

Review of: The joint evolution of lifespan and self-fertilisation

The authors develop evolutionary models of the evolution of the selfing rate and plant life-history. First looking at the evolution of the lifespan, than the mating system, then both. The results are straightforward - as modeled, the extent of inbreeding depression is (much) higher for perennials than annuals, because the costs of inbreeding depression are approximately multiplicative with lifespan. Because inbreeding depression increases with lifespan, they find that perennials should be outcrossing. Similarly, because sellers can trade their letter life inbreeding depression for more success early in life, they selfers should evolve to be annuals. The results are intuitive and well described, and the model predicts a well known observation. This seems like the beginning of a potentially interesting result!! However I do have some concerns. These concerns include (1) Whether then current simple model is useful without the complex realities of (2) The consistency of inbreeding depression across mating system, (3) The lack of senescence. I also wonder (4) if the model is necessary to

explain the correlation found in nature.

Before discussing these issues, I note a mysterious omission from the results, that would help readers. Specifically, the major assumption (?or maybe result?) of this manuscript is that the realized inbreeding depression increases with longevity. However, this result was not stated particularly clearly. A simple graph plotting the lifetime inbreeding depression as a a function of the survival reproduction trade-off (perhaps clearly delineating the classic delta = 1/2 threshold) could clarify this result.

(1) Whether then current simple model is useful. While it is often for theorists to criticize "verbal models" the parameterization of the model (that perennials have a higher level of inbreeding depression, and the results follow simply from this assertion. Similarly selfers can reduce their genetic load by taking their substantial later life inbreeding depression for early life fitness (a classic result in senescence literature... see williams 1957).

While a simple model with easily predictable results can serve some purpose, this seams like more of an idea for a paper than a complete manuscript. I leave it to the authors and editor to decide whether the results here are sufficient for a brief note, or if they would only be useful as a portion of a more extensive manuscript. Perhaps one way to think about this is to ask if there where any surprising results that where not immediately expected by the authors. If the answer is "yes" they may want to share/highlight these.

Another thing I'm having trouble thinking about is if the authors have shown that perennially prevents the evolution of selfing, or if high inbreeding depression precludes the evolution of selfing (which is well known), and then parameterize a model where lifetime inbreeding depression increases with expected lifespan. An "apples to apples" comparison would fix the total expected lifetime inbreeding depression to not differ by life-history, and then see if life history & mating system themselves (independent of the increased inbreeding depression experienced in longer lived species that is asserted in this model) itself has any causative effect, or if the result is simply a consequence of higher effective inbreeding depression with lifespan. Of course, it is unclear if an apples to apples comparison is appropriate, or if the authors should just say "we've sensibly parameterized a model which shows that lifetime inbreeding depression is elevated in perennials"

(2) The consistency of inbreeding depression across mating system The authors note this assumption. It is quite hard to know what to do here. If increases in selfing rate severely impact inbreeding depression (by purging or fixing the load), then the results can be tempered (if inbreeding decreases inbreeding depression), or removed (if inbreeding fully purges the load). Alternatively, if habitual selfing results in outbreeding depression), or enhanced (if fertility/fitness increases with age) the results would be reversed.

However things get more complex - for example, in a community setting there is a major difference between a fixed load (in which this species could be replaced by another) and a purged load, while in population genetics models with stable n, there is no such difference. Thus while the model as set up is clearly wrong, it's wrongness may better reflect true biology than a proper model.

Given these challenges, and the concern that without a deeper thought the paper is pretty thin/predictable, thinking hard about allowing the load to change with mating system could make this a more substantial contribution.

(3) The lack of senescence / stand decline.

As the authors introduce at the end of the manuscript (line 325) the models assume no senescence. Clearly including senescence would act to functionally decreases the effective inbreeding depression in maturity and make the proposed effect less severe (although the authors could, for example play with the functional form of senescence and inbreeding depression as well). Again adding some reality tooth's manuscript would flash it out some (although its not clear that this would aaa results that aren't predictable a-priori (as I just predicted them).

(4) Is the model is necessary to explain the correlation found in nature.

The work is motivated by the association between selfing and lifespan observed in nature. While the results of the model generate this correlation, it is unclear if the model results have anything to do with observations in nature. Above I discussed some of the shortcomings in the modeling. Here I ask if the model is necessary. Selfing plants often live in ephemeral habitats which directly change the probability of surviving to the end of

season ("high extrinsic mortality"), and consequently there is no survival across years, even for perennials. This observation could be interpreted as concistent with this model OR it could be argued that these environments are the ones in which selfers thrive and/or can persist in the face of e.g. mate/pollinator limitation. And therefore the "predictions" of the model are generated by ecological factors unrelated to the predictions, rather then the genetic scenario modeled by the authors.

See the introduction of Emms et al 2018 (a paper of tangential relation to this idea), for some key references.

Another reason why it is unclear if this model is necessary to explain the observed association between mating system and an annual life history is noted by the authors - 'long-lived species may endure significantly more mitotic mutations throughout their lives owing to their overall larger stature, which could result in an increase in inbreeding depression as plants do not have a separated germline.' It is important to separate whether a mode plausibly predicts some pattern (which this model does, at least as parametrized) and if the processes described in a model paly a causative role in generating this pattern (which this may or may not due, even if the model is correctly parameterized).

(5) Additionally there are some deliberate misstatements / incorrect citations.
For example Charlesworth and Willis do not suggest "Inbreeding depression is generally thought to be caused by recessive mildly deleterious mutations segregating at low frequencies in populations". In fact the point to evidence many rare large effect recessives (although they acknowledge that modest effect partial recessives may also play a role in inbreeding depression).