

Comparison of Related Parthenogenetic Species with Unique Mechanisms to Backtrack the Origin of Meiosis

Ben Webb
Evolutionary Analysis

Project Summary

Overview

Reproductive methods are an extraordinarily variable trait across all biological species. One of the fundamental parts of eukaryotic reproduction is with genetic contributions from more than two individuals. The contribution from multiple individuals greatly increases the adaptive fitness of an organism. It is unknown however, the exact origins of meiosis. Parthenogenetic species are species that perform meiosis but undergo embryogenesis of a viable offspring without fertilization. *Arabidopsis thaliana* is a species of plant with numerous microspecies that undergo parthenogenesis at different steps in meiosis. Looking at the fitness effects of these highly similar forms of parthenogenesis, allows for the comparison and insight into the broader impacts and importance of each step of meiosis. The fitness values from different reproductive specific fitness algorithms will be used to estimate the fitness importance of meiosis up until the point of parthenogenesis. The fitness values will be used to create an evolutionary timeline of meiosis inclusive of the fitness of each step. These fitness values and mechanisms will be grouped and compared to phylogenies to see if there is any congruence within and between mechanisms of parthenogenesis. Congruence between mechanisms and phylogenies will allow fitness assignment to individual parts of meiosis. Looking at alterations to complex extant phenotypes allows for insight into the origins of their precursors that existed prior to human's ability to monitor them, opening the possibility to infer the origins of nearly any phenotype.

Intellectual Merit

These methods rely on previously demonstrated algorithms for fitness estimation. These algorithms will first be experimentally verified to view how well they reflect the broader fitness state of an organism. Furthermore, this work only aims to see if the detection of these phenotypes is even possible. The relationship between the fitness estimation of each form of parthenogenesis is predictive and exploratory. This investigation aims to start by validating the plausibility of the methodology, and few conclusions will be made beyond attempting to assign an age to a phenotype based off the fitness of the phenotype. In order to gain more significant and specific knowledge about individual steps within meiosis, further research will need to be done experimentally controlling for the states in the context of the estimated evolution of meiosis to be able to draw any significant causative conclusions.

Broader Impacts

Meiosis is a fundamental part of biology and inheritance problems, but the evolution of the trait itself is still unknown. All species must undergo some form of reproduction. Gaining more understanding of a trait as omnipotent as meiosis allows for the application to a myriad of different species. The general process could even be applied to complex phenotypes that are less contained to a specific part of cell cycle than meiosis, will a more obscure evolutionary origin. By better understanding the origins of a process that is fundamental to biology, we can better understand how meiosis enhances the ability of organisms to evolve, and how it may change in the future as the rapid adaptability of organisms becomes more and more important.

Project Description

Background

Evolution by natural selection is the idea that only a specific subset of those who are best adapted to an environment in a population will survive to produce the succeeding generation. The phenotypic traits that determine who within the population will survive to reproduce, are passed on to the following generation resulting in a shift of the phenotypic proportion in that population. A significant aid in the adaptability of species phenotypes between generations is meiosis, allowing for outcrossing or sexual reproduction between two individuals who both contribute a portion of their genetic material to the offspring. It has been shown that outcrossing is better at removing deleterious alleles from the population (McDonald et. al 2016) as well as interrupting genetic hitchhiking to allow for genes to be selected for independently of one another (Freeman and Herron 2007). Despite the benefits of more efficient selection of phenotypes when producing offspring, species that perform asexual reproduction still exist.

Asexual reproduction is reproduction in which offspring arise from a single individual. It results in higher potential for exponential growth than in meiotic outcrossing, where half of the offspring in sexual species are unable to produce offspring of their own (Hörandl 2009). Apomixis is asexual reproduction in plants that once performed sexual reproduction (Albertini 2001). A subset of apomictic species are parthenogenic species, which are species that undergo meiosis to form an ovum, but develop in the absence of fertilization from another individual. There are a multitude of different underlying parthenogenic mechanisms due to the complexity of meiosis (Autran 2011). Each mode of reproduction can be seen as a variable phenotype across different species. This results in multiple closely related microspecies, with a significantly different reproductive method, i.e. reproductive isolation. By looking at the state of the genome for each microspecies in the context of the step of meiosis that the parthenogenic phenotype manifests itself, a better contextual of meiosis can be created with the ability to compare different steps within the process.

The origins of meiosis are still not entirely known (Albertini 2019). In part, this is because the full mechanism of reproductive signaling are not fully understood. In addition, a significant amount of evolutionary time has passed since meiosis was a novel phenotype. It is possible that a variant mechanism of meiosis, resulting in parthenogenesis, could be an *atavism* for a reproductive method that existed before meiosis as it is known today. Fitness values are normalized to this evolutionary moment, and it is just as possible that a perceptively novel phenotypes could be remnants of an ancestral phenotype that has yet to be fully removed from a population. In this perspective, parthenogenesis is an atavism manifesting as a meiotic failure as opposed to a random mutation resulting in a truly novel phenotype.

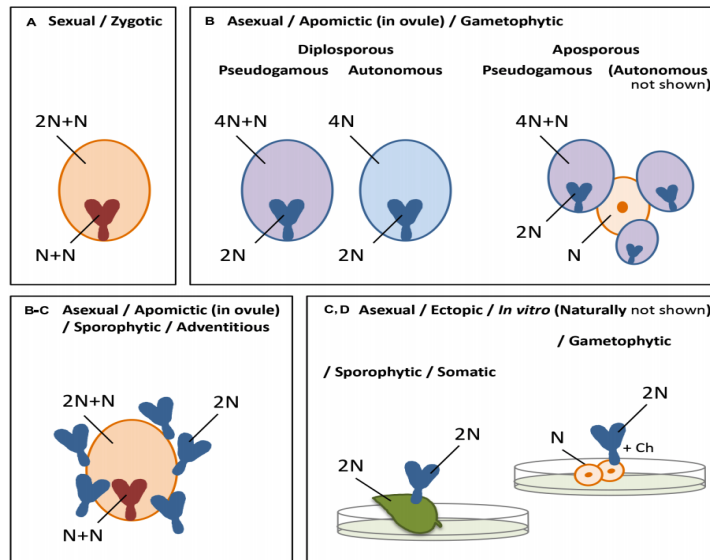


FIGURE 1 Summary of the different forms of embryogenesis in plants, showing the embryo and endosperm originated from a mature embryo sac (**A,B**) or the embryo ectopically (**C,D**) after sexual (**A**) or asexual (**B-D**) reproduction, with orange indicating the sexual process, blue the asexual or apomictic process, pink apomictic reproduction with fertilization of the central cell, and N = chromosome set after reduction division: (**A**) *zygotic embryogenesis*, involving chromosome reduction (N) and gamete fusion ($N+N$ for the embryo, $2N+N$ for the endosperm), (**B**) *apomictic embryogenesis*, occurring in the ovule, either *gametophytic apomixis* in which an embryo sac arises from an unreduced megaspore (diplospory) or sporophytic cell of the ovule, usually adjacent to a sexually derived spore or developing embryo sac (apospory), and parthenogenetic (spontaneous) embryo development and autonomous (spontaneous) or pseudogamous (after fertilization of the central cell) endosperm formation, or *sporophytic apomixis* in which the embryo arises directly from a sporophytic cell of the ovule, often as polyembryony and alongside a sexually derived embryo and endosperm (**C**) *somatic/sporophytic embryogenesis*, involving ectopic embryo development from sporophytic cells, and (**D**) *gametophytic embryogenesis*, idem from a gametophytic cell. The latter two (**C,D**) omit the formation of an embryo sac, endosperm, and a seed coat, and occur naturally, for example, from leaf margins or ovular cells (**C**), gametophytic tissue in lower plants or, e.g., a synergid (**D**), but are particularly known from *in vitro* embryogenesis in which embryos are formed in culture, after external induction, particularly from protoplasts, leaf, the hypocotyl or other plant tissues (**C**), or

Arabidopsis Thaliana (Common Name, Thale Cress) was the first plant genome sequenced and is commonly used as a model organism. Individuals within this species perform a majority of the unique types of asexual embryogenesis (Figure 1, from Vijverberg 2019). While almost all members undergo meiosis, it is estimated that individuals only outcrosses at a rate of 0.3% (Abbott 1989). Furthermore, linkage disequilibrium in the *A. Thaliana* genome produces estimates that that self-pollination arose about 1 million years ago from a pre-meiotic ancestral phenotype (Tang 2007). The short evolutionary time means that the primary differences between each microspecies, outside of habitat specificity, will likely be driven by the variable meiotic factors.

Uyenoyama et al. attempted to create a fitness algorithm to compare outcrossing and parthenogenesis. The algorithm is a measurement effects of the relatedness between parent and offspring seen through allelic substitution as a function of the adaptability of each species genome in response to the need for selection. One of their primary goals was to explain the persistence of parthenogenetic forms of reproduction in the context of sexual forms. The basis of their equation indicates that the offspring of the outbred system only need to have equal cost to the deleterious effects of parthenogenetic reproduction in order to balance the cost of outbreeding. The myriad of reproductive methods merits a further and more quantifiable examination of the fitness effects of both outcrossing and parthenogenesis.

Objectives

My research will be focused on investigating unique parthenogenic methods can be used to understand the important of individual steps in meiosis. I will also be estimating the relative fitness of different forms of parthenogenesis to try to better understand the sequential steps resulting in meiosis and sexual reproduction.

The first objective of this experiment is to evaluate different forms of quantification of fitness cost associated with different types of reproduction to be able to detect between different polymorphic versions of parthenogenesis. This will be done by comparing the fitness estimates based off of the reproductive mechanisms alone to measures of fitness that do not explicitly consider reproductive

strategies. Estimating fitness from reproductive habits is a predictive model, attempting to quantify just one aspect of a species fitness, while a majority of fitness estimates are created from past knowledge and survival of the organism. I hypothesize that fitness estimates based off of each reproductive strategy will be unique to the mechanism, with novel deleterious mechanisms having distinguishably lower fitness values from reversals.

The second objective is to evaluate the feasibility of using the estimated fitness values resulting from the parthenogenic reproductive fitness models to create a timeline of meiosis. With the ability to assign a fitness estimate to each step in meiosis as a product of different parthenogenic methods, it is then possible to extrapolate back to the origins of meiosis. I hypothesize that because the fitness of a species will on average increase over time, the higher the fitness values for a given form of parthenogenesis, the more likely it will be a recent reversal resulting in the loss of meiosis.

Methods

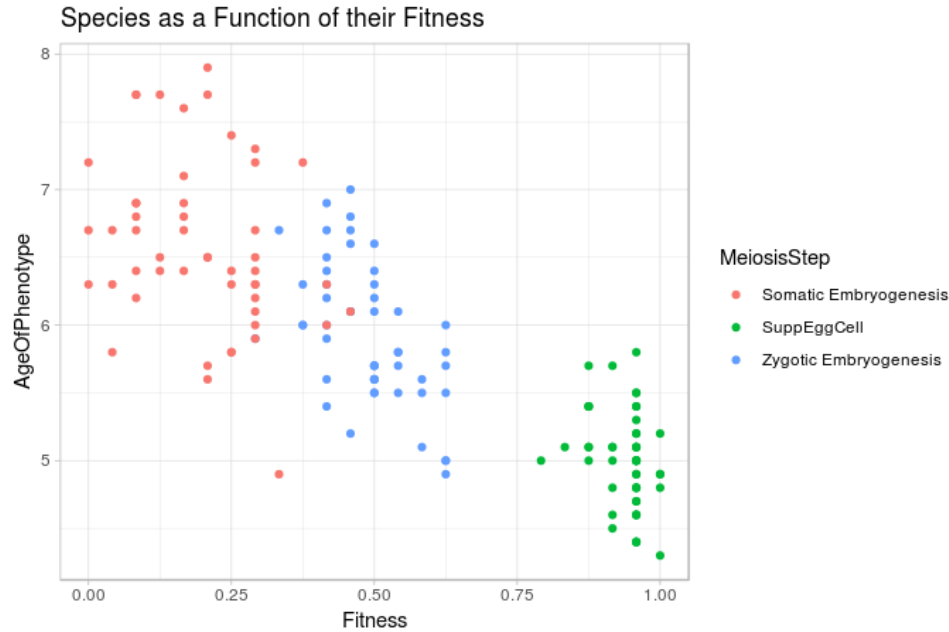
Objective One

The first step is evaluating the efficacy of the applying a fitness cost to distinguish between different types of reproduction. Creating a method to estimate fitness across unique reproductive strategies is uncommon, with a majority of quantitative genetic algorithms created within the context of only one type of reproductive method or inclusive of a whole organism's fitness. This will be done by first creating baseline fitness estimations for the *A. Thaliana* species that undergo parthenogenesis looking at common fitness markers of microspecies genomes from the NCBI database (Akiyama et al. 2004). Which will then be compared to the result of applying the Baldwin effect to a NK model (Bull 2017, Kauffman 1989) and the algorithm deduced by Uyenoyama which relies on the known steps of meiosis that are performed.

The Baldwin Effect is the phenotypic plasticity allowing an organism to demonstrate fitness not seen directly in its genome. When applied to an NK model, which estimates fitness based on the length of the genome and the number of genes within the genomes that have an effect on the model's fitness, the Baldwin effect can be used to evaluate the fitness of the species. As the fitness of a species increased, the Baldwin effect will be less significant.

Objective Two

To further evaluate the efficacy of viewing the species from a reproductive perspective, phylogenetic groups will be made based off of the genetic signals of reproduction. To view how well the groups of parthenogenic mechanisms are defined, a Naïve Bayes classifying algorithm will be run on each group and then all sequenced species will be classified. This will simply group microspecies based off their parthenogenic mechanism but will not draw relationships between different mechanisms. The Naïve Bayes theorem will also be able to provide a confidence interval of the fitness for each parthenogenic method, to allow for comparison of the mean fitness of each mechanism. As the mean of the confidence interval decreases, I expect the particular mechanism to be more ancestral. The novel deleterious mechanisms are expected to fall into their own class.



Expected Figure 1. Different Subspecies of the *A. Thaliana* species and their associated fitness values. There is a clear grouping between the type of parthenogenesis performed (MeiosisStep) and the Fitness and Age estimation of the phenotype (in tens of millions of years).

The grouping of parthenogenic methods will then be added to a maximum likelihood phylogenetic tree of these microspecies built from genomic data. If the assigned fitness values group together onto the phylogenetic tree, estimation of which polymorphic phenotypes are remnants of the past as well as the age of the atavistic phenotype based on the different fitness values of traits that fall into this category, to propose a sequential origin of meiosis across evolutionary time.

It is possible that detection of the fitness of the different reproductive strategies will not be possible from a phylogenetic tree and the fitness values of unique reproduction methods algorithms. These methods all assume that there will be a signature associated with a process that is similar in terms of the allelic contribution to the offspring, with the differences coming in the number of mechanisms prior to embryogenesis. This could be in part because the method of determining the fitness cost of reproductive methods does not account for the subtle differences to the point in meiosis at which there is a deviation.

Conclusion/Discussion

Any reproductive variant that appears to have an associative fitness between different species or has similar genetic markers within the genome will be further evaluated to measure the broader evolutionary implications of these stable but low frequency genomes in nature. Understanding the formation of a fundamental process in biology will allow for inference into ancient phenotypes that are long gone. Synapomorphies are treated with the same atavistic value as their apomorphic counterparts will have because they both confer some sort of phylogenetic and thus potential atavistic characteristic. This study seeks to both attempt to create and validate methods to predict how different reproductive mechanisms manifest themselves over time. Based on the ability to predict the fitness associated with which stages of meiosis reach completion as well as the age of that phenotype, I hypothesize that it should be possible to create an evolutionary timeline of the evolution of meiosis. If successful, it would also be

possible to try to detect other polymorphic variants of a trait that is less explicitly hierarchical to better understand ancestral species that do not exist today.

References

- [Abbott](#), R. J., & Gomes, M. F. (1989). Population genetic structure and outcrossing rate of *Arabidopsis thaliana* (L.) Heynh. *Heredity*, 62(3), 411-418.
- [Akiyama](#), Y., Conner, J. A., Goel, S., Morishige, D. T., Mullet, J. E., Hanna, W. W., et al. (2004). High-resolution physical mapping in *Pennisetum squamulatum* reveals extensive chromosomal heteromorphism of the genomic region associated with apomixis. *Plant Physiol.* 134, 1733–1741.
- [Albertini](#), E., Barcaccia, G., Carman, J., Pupilli, (2019) Did apomixis evolve from sex or was it the other way around? *Journal of Experimental Botany*.
- [Albertini](#), E., Porceddu, F., Ferranti, L., Reale, G., Barcaccia, B., Romano, B., et al. (2001). Apospory and parthenogenesis may be uncoupled in *Poa pratensis*: a cytological investigation. *Sex. Plant Reprod.* 14, 213–217.
- [Autran](#), D., Baroux, C., Raissig, M. T., Lenormand, T., Wittig, M., Grob, S., et al. (2011). Maternal epigenetic pathways control parental contributions to *Arabidopsis* early embryogenesis. *Cell* 145, 707–719. doi: 10.1016/j.cell.2011.04.014
- [Bernstein](#), H., Bernstein, C., & Michod, R. E. (2011). Meiosis as an evolutionary adaptation for DNA repair InTech.
- [Bull](#), L., (2016;2017), The Evolution of Sex through the Baldwin Effect. *Artificial life*. 23:481-492.
- Freeman, S., & Herron, J. C. (2007). *Evolutionary analysis*, Chapter 8.3 . Upper Saddle River, NJ: Pearson Prentice Hall.
- [Hörandl](#) E. (2009) Geographical Parthenogenesis: Opportunities for Asexuality. In: Schön I., Martens K., Dijk P. (eds) *Lost Sex*. Springer, Dordrecht
- Kauffman, S., Weinberger, E., (1989) The NK model of rugged fitness landscapes and its application to maturation of the immune response, *Journal of Theoretical Biology*, Volume 141, Issue 2, Pages 211-245
- McDonald, M. & P. Rice, Daniel & M. Desai, Michael. (2016). Sex Speeds Adaptation by Altering the Dynamics of Molecular Evolution. *Nature*. 531. 10.1038/nature17143.
- [Tang](#), C., Toomajian, C., Sherman-Broyles, S., Plagnol, V., Guo, Y., Hu, T. T., Nordborg, M. (2007). The evolution of selfing in *Arabidopsis thaliana*. *Science*, 317(5841), 1070-1072.
- [Uyenoyama](#), M. K. (1984). on the evolution of parthenogenesis: A genetic representation of the “cost of meiosis”. *Evolution*, 38(1), 87-102.
- [Vijverberg](#), K., Ozias-Akins, P., & Schranz, M. E. (2019). Identifying and Engineering Genes for Parthenogenesis in Plants. *Frontiers in plant science*, 10, 128.