PERSPECTIVES



Meiosis solved the problem of gerrymandering

J. ARVID ÅGREN^{1,2*}, DAVID HAIG¹ and DAKOTA E. McCOY^{1,3,4}

¹Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA

²Department of Evolutionary Biology, Uppsala University, 75236 Uppsala, Sweden

³Hopkins Marine Lab and Department of Materials Science and Engineering, Stanford University,

Stanford, CA 94305, USA

⁴Department of Biology, Duke University, Durham, NC 27708, USA

*For correspondence. E-mail: arvid.agren@ebc.uu.se.

Received 14 March 2022; revised 28 June 2022; accepted 11 July 2022

Abstract. Gerrymandering, the structuring of voting districts to favour certain politicians and political groups, undermines fair elections and presents a serious challenge to democracy. We introduce a solution to gerrymandering inspired by the biological process of cell division in sexually reproducing organisms, meiosis, in which the boundaries of electorates are frequently redrawn by randomizing algorithms. By demonstrating the deep parallels between meiosis and John Rawls's concept of a 'veil of ignorance', we also show how one of the biggest threats to the integrity of meiosis—selfish genetic elements, genes that promote their own transmission at the expense of organismal fitness—can inspire another potential advantage to frequent random redistricting.

Keywords. genetic conflicts; selfish genetic elements; randomization; John Rawls.

'Many of our most serious conflicts are conflicts within ourselves.'.

- J. Rawls, 2001, p. 30.

Introduction

Parliamentarians and genes both need to cooperate, and both parliaments and genomes suffer when group members behave selfishly. So how can selfish behaviour be kept in check to prevent the degeneration of the collective? In the realm of politics, moral philosophers often refer to John Rawls's influential treatise *A theory of justice* (Rawls 1971). Central to Rawls's notion of a fair society is the concept of a 'veil of ignorance', a moral reasoning tool that suggest that we should make decisions about the structure of society as-if we did not know how we would personally be affected by them.

Evolutionary biologists have shown that Rawls's veil of ignorance also applies to genetics. One example is meiosis, the production of gametes in sexually reproducing organisms, where selection has favoured adaptations that restrict selfish genetic behaviour and promote fairness during transmission (Ridley 2000; Okasha 2012; Queller and Strassmann 2013). Meiosis ensures fairness by drawing a Rawlsian veil. Here, we argue that this parallel can inspire new techniques to help us design a fairer society. Specifically, we use insights from meiosis to address an acute challenge to fair governance: gerrymandering.

The problems and politics of gerrymandering

Gerrymandering refers to the drawing of voting districts to favour particular politicians or political parties (figure 1). First coined in the *Boston Gazette* in 1812, the practice was named after the politician Elbridge Gerry who drew salamander-shaped districts to bias elections in his own favour. Gerrymandering corrupts democracy by protecting incumbent politicians from meaningful democratic challenges. Therefore, the outcomes of elections and the control of power is determined not by the popular vote but by politicians currently in power. J. A. Ågren et al.



Figure 1. Contemporary examples of gerrymandering in the US. (a) The 35th congressional district of Texas and (b) the 4th congressional district of Illinois. (c) The shape of voter districts may affect the outcome of the election. Consider a state with 50 precincts that is to elect five representatives (top left). Citizens are 40% green-leaning and 60% purple-leaning. By drawing five same-shaped districts, purple wins 3 and green wins 2 (delivering the state to purple). Alternatively, the districts may be drawn in different shapes (gerrymandered; bottom left) to deliver all five districts and the state to the purple majority. Such a result is arguable a distortion given that 40% of the electorate will disagree with their representatives if the all purple are elected. Alternatively, the districts may be drawn in different shapes (gerrymandered; bottom right) to deliver three districts, and the state, to the minority green. In this scenario, only two of the elected representatives will be purple—a distortion because then the minority (green) will be in nonrepresentative control of the state. As this toy example illustrates, gerrymandering is a powerful strategy to distort election results. Figure designed by Esther Fadumiye.

Empirical observations suggest that this is not just a hypothetical scenario. Partisan gerrymandering prevents legislative action that would be popular among the whole electorate. Take, for example, the issue of gun control in the United States. In 2019, a large majority of Americans supported stricter gun control measures, including background checks (supported by 88% of Americans), banning high-capacity magazines (71%), and banning assault weapons (69%) (Tausanovitch *et al.* 2019). Yet, the same

study revealed that in four states (Pennsylvania, Michigan, North Carolina, and Wisconsin) gun control reform has been blocked, despite being supported by the majority of voters in these states. At the time of writing, all the four states were under minority rule due to gerrymandering. Because of gerrymandering (and other polarizing forces), elected officials thus represent the interests of the few (opponents of gun control) rather than the many (advocates of gun control) (Smith 2020).

Old and new solutions to gerrymandering

It is difficult to articulate a completely fair method of drawing districts. By its very nature, fairness depends on numerous philosophical assumptions (Katz *et al.* 2020). For example, is it better to provide homogenous districts where state-wide minorities can gain representation, or heterogenous districts that represent microcosms of the broader state?

Several solutions to the problem of gerrymandering are built on the insight that it is easier to spot cheating than to define fairness. One category of solutions uses mathematical approaches to identify irregular districting size and shape, which could suggest unfairness (Tapp 2019). With these methods, one can detect gerrymandering by determining whether election performance is symmetrical, i.e., whether both parties need the same number of votes to win (rather than, say, one party needing 40% of votes to win while the other party needs 60% of total votes to win) (Duchin 2018). For example, in the 2010 election, 60 out of 99 electorates in Wisconsin returned Republican representatives, despite Republicans receiving fewer state-wide votes than Democrats, a result likely due to the heavily gerrymandered districts (Herschlag *et al.* 2017).

Other solutions have to do with how districts are designed. Probably the most commonly proposed solution to gerrymandering is to transfer the power to draw districts from elected officials to an independent, nonpartisan, body. When this solution was implemented in Canada in the 1960s, it practically ended the country's problems with gerrymandering (Gaughan 2013).

We propose a further modification, inspired by the biological process of meiosis, in which the boundaries of electorates are frequently redrawn by randomizing algorithms. Fair meiosis aligns the fitness interest of genes within a genome and frequent random redistricting has two democratic advantages. The first is the elimination of gerrymandering and the second is breaking up long-term associations between particular politicians and particular voters. One of the dilemmas faced by a politician is balancing the good of the nation, most of whose members do not vote for the politician in question, against the parochial interests of the electorate whom the politician represents. An advantage of frequent reshuffling is that a politician must shape their voting record to appeal to a wider electorate because future electors are thereby rendered less predictable.

How meiosis solved the problem of gerrymandering

A sexually reproducing organism is a temporary compromise between genes whose fitness interests may or may not align. An individual inherits genes from its father and from its mother, and for the individual to be evolutionary successful these genes must act in harmony before going their separate ways in the next generation. For most genes, the best way to increase their chances of being transmitted is therefore by improving the (inclusive) fitness of the whole organism.

Not all genes, however, act fairly to improve whole-organism fitness. Some genes, usually referred to as selfish genetic elements (Burt and Trivers 2006) are able to interfere with the laws of inheritance to promote their own transmission, even if it comes at the expense of organismal fitness. Just like gerrymandering, selfish genetic elements are not just theoretically possible but are in fact a dominant component of plant and animal genomes. The presence of selfish genetic elements is often associated with a reduction in fitness and organisms have evolved various ways to deal with them.

The most important strategies to deal with selfish genetic elements are the acts of randomization involved in the process of meiosis (figure 2). During meiosis, the chromosome number is halved, so a given gamete inherits only one copy of each gene. Sex thus means that not all genes are inherited, but that a given gene copy has a 50% chance of being transmitted. The fact that a gene copy has no information about whether it will be transmitted or not means that the best behaviour from a gene's perspective is to support whole-organism fitness. This is also why meiosis is often described as 'fair' and it is crucial to align the interests of genes with that of the whole organism (Leigh 1971; Haig and Bergstrom 1995; Frank 2003; Veller 2022).

Yet, some selfish genetic elements can still subvert fairness by banding together to enhance their own odds of transmission. For example, *Drosophila melanogaster* individuals carry a cabal of genes known as the *Segregation Distorter* (*SD*) complex, which interferes with the production of sperm. Males carrying *SD* produce offspring that nearly all inherit *SD*, rather than the 50% that would be the case if meiosis was fair.

This is where another fairness enforcing act of meiosis, crossing over, becomes relevant. Crossing over breaks up gene combinations, which causes genes to be inherited independently of each other (figure 2). This act of randomization may hold the key to why *SD* is typically found at such low frequencies in natural populations (Haig and Grafen 1991). Molecular genetic analyses have revealed that the *SD* complex is actually made up of two tightly linked loci, both of which are needed for the drive to be successful. Crossing over, then, destroys this linkage and so restores fairness to meiosis.

Meiotic randomization therefore ensures that the phenotypic effects of genes evolve to promote the collective (organismal) good. Because individual genes have no information whether they will be inherited by particular offspring, or with which other genes they will be inherited, this aligns the interests of all genes of the genome, in part by breaking-up selfish cabals of co-inherited genes that might conspire against the collective.

How can the insights from meiosis help with the problems of gerrymandering? Inspired by the process of crossing over, district boundaries could be randomly redrawn for every

J. A. Ågren et al.



Figure 2. A simplified version of meiosis showing the key acts of randomization: crossing over and the fair halving of chromosome number. In diploid organisms, each individual carries two chromosomes (shown here in green and purple). The two sister chromosomes line up and exchange genetic material during crossing over. This is followed by two cell divisions, the latter which results in four haploid gametes. Figure designed by Esther Fadumiye.

election. From year to year the population size per district will be held constant, and the shape of the districts constrained. For example, in the state of Texas with a population of just under 30 million and 36 seats in the US House of Representatives, 36 'random' points could be scattered throughout the state, with the distance between points reflecting local variation in the population density of voters (figure 3). Algorithms then randomly draw boundaries around each point to establish the 36 districts of equal population size. A more radical option would be to create districts composed of multiple noncontiguous sub-sampled areas and politicians could be randomly assigned to districts each election cycle. It would be interesting to model how these solutions compare to other quantitative approaches, such as Tapp (2019).

This method prevents extreme gerrymandering by rerolling the districting dice every election. Cabals of the few cannot therefore count on seeing the same 'lucky tail' of all possible districts (as in, for example, Wisconsin). It also breaks up districts that were organized by historical demographics, which may no longer be relevant. If a representative cannot be certain who they will have to please after the next redistricting, they will have to support positions that also will be popular in neighbouring communities, analogously to how most genes act to promote organismal fitness rather than selfishly to bias their own transmission. If there are fewer safe seats and more contested seats whose voters are continually being reshuffled, we predict that a successful long-term political career will require voting for legislation that appeals to a wider swathe of voters.

The maxim that 'all politics is local' reveals a tension between the costs and benefits of long-term associations between representatives and particular voters. Such associations can be portrayed as unhealthy. The practice of 'earmarking' in which special provisions are written into bills to benefit particular representatives has been frequently derided as they typically serve the politician's local electorate or influential donors rather than the nation. A prominent American example of this practice is the socalled Bridge to Nowhere in Alaska. As long as the Golden Gate Bridge and higher than the Brooklyn Bridge, the bridge was proposed to connect the town of Ketchikan (population 90,000) to Gravina Island (population 50) to the tune of 398 million US dollars. After initially being approved for federal funding, public attention brought about by the 2008 Presidential election led to the project's cancellation.

District randomization would reduce the incentives for such local 'pork-barrel' politics. However, politicians who are attuned to local interests can also achieve important changes. The representative for a stable electorate can be well-liked, invested in local growth, and committed to long-term change through decades of sustained work with local stakeholders. Our proposal could be seen as undermining this kind of long-term government service. Further, districts, and by association their representatives, that are



Figure 3. Districts could be re-drawn each election year based on population density. (a) Existing congressional districts in Texas. (b) Population density in Texas; each dot represents 100 people. (c) New districts could be drawn by randomly placing dots in hidden polygons that each capture $\sim 1/36$ th of Texas's population (here, >700,000 people per dot). Algorithms could then draw new nonoverlapping districts (of the equal population) around these dots. Figure created using R packages ggplot2, tidycensus, and dplyr (Wickham 2016, 2022; Walker *et al.* 2021).

stable from election to election may better allow local organizers to campaign for change. Regular changes could result in extra work as organizers scramble to build lasting relationships with elected representatives. Finally, repeated redistricting may be perceived as confusing, which could frustrate voters and reduce voter turnout.

Data accessibility statement: Code is deposited at https://github.com/ReallyMcCoy/Meiosis_and_Gerrymandoring/.

Conclusion

Democracy rests on the principles of fairness and representation. Elections should be free and parliamentarians ought to represent popular opinion. Gerrymandering is but one example of how this process can be distorted in selfish ways by those already in power. Like parliamentarians, genes need to cooperate, and the function of both genomes and parliaments may suffer from selfish behaviour. Humans have long taken inspiration from biology for engineering and design, from kingfisher-inspired bullet trains to self-cooling buildings modelled after termite mounds. Here we extend the idea of biomimicry to politics: meiosis-inspired voting systems can create a fairer society. We have discussed meiosis, a form of randomization that helps make genomes fairer, as an example of Rawls's veil of ignorance to explore what biology can teach politics. Examples such as in the selfish *SD* gene complex in fruit flies that helps itself but actively harms whole-organism reproductive fitness reveal just how destructive the consequences of failing to reign in selfish behaviours can be (Ågren *et al.* 2019). However, as demonstrated here, biology also offers solutions for how to promote fairness.

Acknowledgements

We thank Esther Fadumiye for help with figure design. This project was funded by The Wenner-Gren Foundations (JAÅ) [WGF2018-0083], Department of Defense [32 CFR 168a], Air Force Office of Scientific Research National Defense Science and Engineering Graduate (NDSEG) Fellowship, 32 CFR 168a (DEM) and Ashford Fellowship (DEM). Stanford Science Fellowship, NSF Postdoctoral Research Fellowships in Biology PRFB Programme, grant 2109465 (DEM).

Authors' contributions

Conceptualization: JAÅ, DH, DEM; writing - original draft: JAÅ, DEM; writing - review and editing: JAÅ, DH, DEM.

References

- Ågren J. A., Davies N. G. and Foster K. R. 2019 Enforcement is central to the evolution of cooperation. *Nat. Ecol. Evol.* **3**, 1018–1029.
- Burt A., Trivers R. 2006 Genes in conflict: the biology of selfish genetic elements, Belknap, Cambridge.
- Duchin M. 2018 Gerrymandering metrics: How to measure? What's the baseline? *arXiv* http://arxiv.org/abs/1801.02064.
- Frank S. A. 2003 Repression of competition and the evolution of cooperation. *Evolution* 57, 693–705.
- Gaughan A. 2013 To end gerrymandering: The Canadian model for reforming the congressional redistricting process in the United States. *Cap. Univ. Law Rev.* **41**, 999.
- Haig D. and Grafen A. 1991 Genetic scrambling as a defence against meiotic drive. J. Theor. Biol. 153, 531–558.
- Haig D. and Bergstrom C. T. 1995 Multiple mating, sperm competition and meiotic drive. J. Evol. Biol. 8, 265–282.
- Herschlag G., Ravier R. and Mattingly J. C. 2017 Evaluating partisan gerrymandering in Wisconsin. arXiv http://arxiv.org/abs/ 1709.01596.
- Katz J., King G. and Rosenblatt E. 2020 Theoretical foundations and empirical evaluations of partian fairness in district-based democracies. *Am. Polit. Sci. Rev.* **114**, 164–178.
- Leigh E. G. Jr. 1971 Adaptation and diversity: natural history and the mathematics of evolution, Freeman, Cooper, San Francisco.

Corresponding editor: DURGADAS P. KASBEKAR

- Okasha S. 2012 Social justice, genomic justice and the veil of ignorance: Harsanyi meets Mendel. *Econ. Philos.* 28, 43–71.
- Queller D. C. and Strassmann J. E. 2013 The veil of ignorance can favour biological cooperation. *Biol. Lett.* 9, 20130365.
- Rawls J. 1971 A theory of justice, Belknap Press, Cambridge.
- Rawls J. 2001 Justice as fairness: a restatement, Belknap Press, Cambridge.
- Ridley M. 2000 Mendel's demon: gene justice and the complexity of life, Weidenfeld & Nicolson, London.
- Smith C. E. 2020 Gun policy: politics and pathways of action. *Violence Gender* 7, 40–46.
- Tapp K. 2019 Measuring political gerrymandering. *The American Mathematical Monthly*. 7, 593–609.
- Tausanovitch A., Parsons C., Rukmani B. 2019 How partisan gerrymandering prevents legislative action on gun violence. *Center for American Progress* https://www.americanprogress. org/issues/democracy/reports/2019/12/17/478718/partisangerrymandering-prevents-legislative-action-gun-violence/.
- Veller C. 2022 Mendel's first law: partisan interests and the parliament of genes. *Heredity*, https://doi.org/10.1038/s41437-022-00545-x.
- Walker K., Herman M., Eberwein K. 2021 Package 'Tidycensus. https://CRAN.R-project.org/package=tidycensus.
- Wickham H. 2016 ggplot2: Elegant graphics for data analysis. https://ggplot2.tidyverse.org.
- Wickham H., François R., Henry L. and Müller K. 2022 dplyr: a grammar of data manipulation. https://dplyr.tidyverse.org.