

Sexual Selection Promotes Ecological Speciation in Digital Organisms

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Abstract

Ecological Speciation is the development of reproductive isolation as a result of divergent adaptation to different environments. As populations diverge, post-zygotic isolation effects such as low hybrid fitness and zygotic inviability are expected to become increasingly dominant. However, for genetically similar incipient species, post-zygotic effects may not be sufficient to enforce a reduction in gene-flow. Models of allopatric speciation predict that pre-mating isolation may play an important role in reinforcing barriers between species, regardless of genetic incompatibilities. However, evidence for these models is mixed, and remains controversial. In this paper, we examine the extent to which pre-mating isolation resulting from divergent sexually-selected traits is sufficient to generate incipient species. We evolved populations of sexually-reproducing digital organisms that use sexual selection to choose their mates. These populations are then divided, and each half allowed to adapt to divergent environmental conditions (allopatry). We then reunited these populations for a single round of mating and measured the rate of hybridization. We found that sexual selection significantly reduces the number of hybrid matings between populations. Further, we found that post-zygotic effects were only minimally present, despite adaptation to distinct environments, and that there was little difference in both pre-mating and post-zygotic effects between distinct sets of environments. We conclude that sexual selection is a strong force for generating incipient species, even while post-zygotic effects have minimal impact.

Introduction

Sexual selection is a mechanism by which individuals of one sex choose their mates based on perceived values of one or more phenotypic traits. Members of the other sex then compete for mates on the basis of those traits. Individuals with the most prominent trait expression tend to have better mating success, passing on those traits to their offspring, and driving greater and greater trait expression (Darwin and Wallace, 1858).

Sexually-selected traits appear to evolve more rapidly than life-history traits (Pitchers et al., 2014; West-Eberhard, 1983; Civetta and Singh, 1998). Thus, divergence of sexually-selected traits may rapidly cause potential mates to discriminate against organisms that do not share desirable

courtship traits (Fisher, 1930; Lande, 1981; West-Eberhard, 1983; Panhuis et al., 2001). Thus, sexual selection may create early barriers to gene-flow between populations with divergent traits. For this reason, sexual selection is an obvious candidate for driving increased species richness (Darwin and Wallace, 1858; Panhuis et al., 2001; West-Eberhard, 1983). However, the role of pre-mating isolation in ecological speciation is controversial and the evidence is mixed (Kraaijeveld et al., 2011; Ritchie, 2007).

The interaction between pre-mating isolation and the process of allopatric speciation is, at the least, complex. It appears to be mediated by many factors, including the strength of selection (Kwan and Rundle, 2010), divergence of allopatric environments (Kwan and Rundle, 2010; Falk et al., 2012), spatial structure (Slatkin, 1987), evolutionary time scales (Hendry et al., 2007), strength of sexual selection (West-Eberhard, 1983), and genetic architecture (Siegal and Leu, 2014; Klemetsen, 2010). In a study of allopatric speciation in seed beetles (Fricke et al., 2010), divergent sexually-selected trait evolution was observed, but the rate of evolution of those traits was reduced when populations underwent strong directional selection. In a study of budding yeast (Leu and Murray, 2006), mating kinetics diverged between independently adapted populations, resulting in pre-mating reproductive isolation.

In contrast, studies of flour beetles (Falk et al., 2012) and fruit flies (Kwan and Rundle, 2010) showed little to no evidence for pre-mating isolation, despite the divergence of sexually-selected traits. However, in both studies, F1 (first generation) hybrids of organisms adapted to different environments displayed asymmetrical fitness reductions between environmental treatments, indicating that adaptations to one environment may not have come at the cost of adaptation to the other. Thus, choice of divergent environments and the genetic architecture of adaptation can have a large impact on experimental outcomes.

In this paper, we show that sexual selection not only promotes pre-mating isolation between divergent allopatric populations, but that the type of divergent environment has little to no significant effect. Further, we show that, at least

in short timescales, post-zygotic effects, such as offspring inviability and hybrid unfitness are largely absent, again, regardless of the type of environmental divergence.

Digital Evolution

Digital Evolution is a branch of Artificial Life devoted to the study of evolutionary principles using self-replicating, evolving computer programs (McKinley et al., 2008). Populations of digital organisms evolve by natural selection; they self-replicate, their genomes undergo heritable mutation, and they compete with their peers for resources and space. While digital organisms do undergo true Darwinian evolution, they do not suffer from many of the drawbacks of natural study systems.

Some of the benefits of digital organisms are particularly relevant to this study. While some experimental evolution studies have been conducted to study the impact of sexual selection on speciation, there are significant drawbacks to using natural organisms. First, identifying the genetic factors that underlie divergent adaptation to different environments is a complicated and difficult task. This in turn, increases the likelihood of choosing allopatric environment pairs that have un-matched responses to selection, or which do not lead to divergent adaptation at all. In digital organisms, however, we can perfectly characterize the features of divergent environments (Ofria and Adami, 2002), and assay the exact strength of selection of a given population against its environment. Further, we can test many different combinations of environments to explore the different dimensions in which divergent evolution can affect speciation.

Further, while insects and yeast have relatively short generation times, performing sufficiently long-term studies to examine the dynamics of speciation is laborious and time-consuming. In digital organisms, studies that would take months or years in natural organisms can be performed in hours or days (Ryan, 1953; Lenski et al., 1991; Anderson et al., 2010; Stearns et al., 2000). This allows us to examine many different ecological combinations, and with many more replicates than would be reasonably feasible for natural organisms.

Methods

Avida Digital Evolution Platform

We used Avida (Lenski et al., 2003) to study the effects of sexual selection on allopatric speciation. Avida is a software system for performing evolution experiments in a virtual world using digital organisms.

Avida organisms are composed of a virtual CPU, with a circular genome of assembly-like instructions (Figure 1). Populations of organisms are placed in individual cells in a toroidal world of fixed size.

Avida organisms are subject to mutation, heritable variation, and selection via reproductive competition, thus populations undergo Darwinian evolution by natural selection.

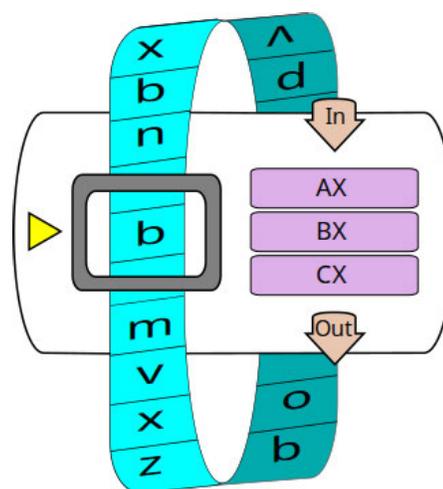


Figure 1: An example virtual CPU from Avida, with a circular genome (blue), three registers (purple), input and output handlers (tan), and an instruction pointer (yellow) indicating the next instruction to be executed (Canino-Koning et al., 2016).

Avida organisms are self-replicating. That is, all the instructions required to copy their genome into a new cell and produce offspring are contained within their genome. By default, during the copy process, heritable errors may be introduced which are then passed on to the offspring. Thus Avida organisms are subject to mutation.

Organisms in Avida compete for space and resources by performing sets of bitwise logical tasks. The organisms that perform a task receive a boost to their execution speed, and this boost gives them an advantage over their competitors. All else being equal, organisms that execute their code fastest tend to reproduce fastest, and come to dominate the population. The tasks and their rewards are also configurable, thus giving the experimenter wide latitude in terms of the types of experiments that can be performed.

Sexual Selection in Avida

The organisms in our evolving populations reproduce sexually, and are able to choose their mates using sexual selection against a single trait. While expression of this trait is not explicitly linked to other life-history traits (such as speed of reproduction), the trait may be influenced by other phenotypic factors over the course of an organism's lifetime. Thus, trait expression, due to pleiotropic interactions, may vary depending on adaptation to varied environments. This model, therefore, allows us to explore the relationship between sexual selection and environmental adaptation.

For this research, we used digital organisms that are individually categorized as male or female. All organisms are permitted to set the value of a sexually selected trait, either as a mate-choice target for the females, or a displayed trait

for the males. This trait is a number that the organisms may set during the normal course of executing their genomes, and ranges between 0 and 127. Specific values on this trait are not inherently good or bad; their worth stems from which particular value the other organisms are searching for and displaying. Because the number is set during genome execution, both the choosiness target in females and the display trait in males are able to evolve. Organisms may also decide to mate randomly. When reproducing, choosy females (those who set a choosiness target) will mate with a male only if there is an exact match between the female target trait and male display trait. Thus, the display trait gives organisms a mechanism to discriminate against potential mates that do not share their trait. In contrast, non-choosy females will mate with a randomly selected available male.

Experimental Design

In order to explore how sexual selection influences speciation, we designed experimental protocols to simulate varying scenarios of allopatric speciation. Allopatric speciation is a model of speciation where a populations become geographically separated, and then after some period of isolation, may encounter each other again. The varying treatment conditions simulate different pairs of divergent environments that the divided populations may encounter and adapt to during their separation.

In the first experimental phase (*sympatry*), we placed the organisms into a single, joint environment where they were given rewards for performing a pre-defined set of logical tasks. We varied the composition of these initial tasks based on the treatment type (see Table 1). We allowed the populations to evolve in this initial environment for 100,000 updates (roughly 3,000 generations). Then, in the second phase (*allopatry*), we divided the populations into two halves, and allowed each half to evolve independently of the other in divergent environments for another 200,000 updates. Finally, in the last experimental phase, we rejoined the populations for a single round of mating.

Each treatment, including the control, is composed of 30 replicates. Each replicate population is evolved in a 60x60 toroidal world, with 3600 available cells. Each population is initially seeded with a single male and a single female organism, with genomes that are 200 instructions in length. These seed organisms (apart from the genetic instruction setting their sex) are identical, and contain only the instructions needed to self-replicate sexually.

Treatment Conditions During the allopatry phase, we subjected the divided populations to a series of different environmental conditions in order to demonstrate the effects of environmental differences or differential adaptation on reproductive isolation.

During the first phase (*sympatry*), *Treatment A* initially provides rewards for all 9 two-input bitwise logical tasks.

These rewards increase commensurate with the complexity of the task (Lenski et al., 2003). In the allopatry phase, we vary the halves by restricting the set of tasks available for reward, with each side adapting to a different subset of options. This treatment simulates environments where the organisms have moved to environments with less rich food-source options.

In *sympatry*, *Treatments B, C, and E* again begin with the a fixed set of logical tasks. But in *allopatry*, we expand the set of tasks available, with each side adapting to a different set of more complex tasks. These treatments simulate environments where options for food sources are expanded in different directions.

Finally, *Treatment D* (*drift*) does not vary the tasks available. All Logic 9 tasks are rewarded in both *sympatry* and *allopatry*. This treatment simulates purely geographic isolation, with no corresponding environmental change. Thus, any resulting differences between the halves could be attributed to drift.

Finally, we include a control. In this treatment, the population is never divided, but allowed to evolve in *sympatry* for the entire 300,000 updates.

Treatment	Sympatry	Allopatry 1	Allopatry 2
A (reduced)	Logic 9 (all)	Logic 9, - ANDN, XOR	Logic 9, - OR, NOR
B (expanded complex)	Logic 9 (all)	Logic 9 + 3AA, 3AB, 3AC, 3AD	Logic 9 + 3BA, 3BB, 3BC, 3BD
C (expanded simple)	Lower 4 (NOT, NAND, AND, ORN)	Lower 4 + OR, NOR, EQU	Lower 4 + ANDN, XOR, EQU
D (drift)	Logic 9 (all)	Logic 9 (all)	Logic 9 (all)
E (expanded braided)	Braided Lower 4 (NOT, NAND, AND, ORN)	Braided Lower 4 + OR, NOR, EQU	Braided Lower 4 + ANDN, XOR, EQU
Control	Logic 9 (all)	N/A	N/A

Table 1: Task environment differences in *Sympatry* vs *Allopatry*

After periods of *sympatry* and *allopatry*, we rejoin the halves of the populations and allow a single round of mating. This final phase simulates renewed contact between the allopatric populations.

Statistics

At the end of the allopatric phase, we measured the fraction of females engaging in mate discrimination. We also measured the rate of hybridization that occurred during the mating round, and calculated the ratio of hybridizing vs non-hybridizing matings that occurred between and within the respective halves. We also performed a random sampling of forced matings between and within the halves and measured the resulting offspring's fitness and viability.

We performed Mann-Whitney-Wilcoxon Rank Sum tests (Fay and Proschan, 2010) to compare means of distributions of mate discrimination vs random mating. We also used MWW Rank Sum with a 5-part Bonferroni correction (Dunn, 1961) to compare hybridization rates between the control and each treatment. Finally, we used MWW RankSum with a Bonferroni correction to compare forced mating fitnesses and viability between hybrid and both in-group forced mating sets, as well as a one-way Anova comparing all fitness and viability measures to each other.

Software and Data Access

Avida is available for download without cost from <http://avida.devosoft.org/>, and specific versions along with data-files to reproduce the experiments described in this paper may be found at <https://github.com/voidptr/avida> and <https://github.com/voidptr/ecal2017>.

Results and Discussion

In order to examine whether sexual reproduction can promote ecological speciation, we evolved six sets of populations of digital organisms for approximately 3,000 generations in sympatry. Then we divided them into six divergent pairs of environments, where they adapted for an additional 6,000 generations (allopatry). We then reunited the population pairs for a single round of mating.

Our experiments demonstrate that not only does allopatric separation allow sexually selected traits to diverge, but that trait divergence occurs regardless of the type of environmental divergence. Further we demonstrate that this trait divergence is sufficient to substantially reduce the rate of hybridizing mating events. We also found that, despite differences in adaptation, the hybridization rate is not significantly different between treatment sets. This indicates that pure allopatry without divergent environmental conditions is sufficient to promote reproductive isolation. Finally, we show that, regardless of allopatric environment type, post-zygotic effects like hybrid unfitness and inviability have negligible impact.

Pre-mating Isolation

Pre-mating isolation is an umbrella term for any mechanism that reduces gene flow between species, prior to mating. These can include differences in mating seasons, separated

mating grounds, and incompatible mating signals. For the purposes of this research, we focused on reproductive isolation caused by incompatible mating signals via divergent sexually selected traits. Here, we measure features that predispose populations toward reproductive isolation, at the end of the allopatric evolution phase.

Use of Mate Discrimination Organisms in our experiments use expression of a particular trait to discriminate between mates. Males express this trait, and females may either choose their mates randomly, or they may choose a mate that matches their preferred trait expression. In order for a population to experience reproductive isolation due to mate discrimination, populations must, of course, perform mate discrimination. We measured the fraction of the population that uses mate discrimination at the end of the allopatric adaptation phase.

We show that our populations use mate discrimination at rates that far exceed that predicted by chance (Figure 2).

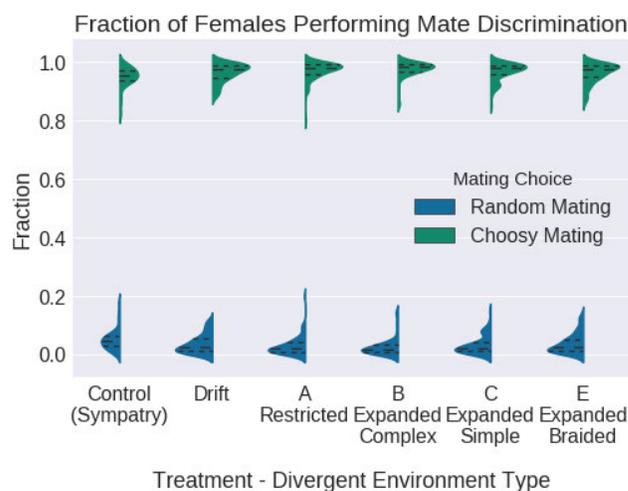


Figure 2: Fraction of females performing mate discrimination across all treatments. All treatments show very high rates of use of mate discrimination. If mate discrimination were under no selection, by chance, we should see similar distributions of Random Mating vs Choosy Mating. (Wilcoxon Rank Sum Test: $Z = -6.65, -9.45, -9.45, -9.37, -9.29$, and -9.29 respectively, $p \ll 0.0001$)

Hybridization Rates In all experimental treatments, we saw significantly reduced hybridization rates as compared to the control. (Figure 3)

Mating rates between the allopatric populations were reduced to approximately half of the in-group mating rates, indicating significantly and substantially reduced gene-flow. The mating rate is directly correlated to the difference in display traits between the populations, because it is the main factor allowing females to discriminate among mates.

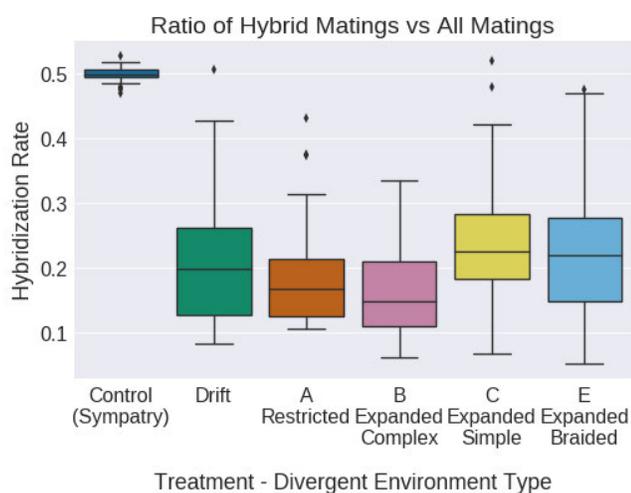


Figure 3: Hybridization rates across all treatments. Every treatment saw approximately 50% fewer hybridization events as compared to the control. (One-Way ANOVA $F(5,171) = 56.49, p << 0.0001$) Hybridization rates between treatments had small, though significant differences, despite large differences between the divided environments. (One-Way ANOVA $F(4,142) = 3.46, p < 0.01$) Of particular interest is the Drift treatment, where identical divided environments still produced dramatically reduced hybridization rates.

Interestingly, the change in display trait, and thus hybridization rates cannot be attributed to differential adaptation. The lack of statistically significant difference between the drift treatment and all other treatments indicates that drift is sufficient to generate differences in display trait, whereas the effect of differential adaptation is overwhelmed when compared to the effect of drift.

Post-Zygotic Isolation Effects

Post-Zygotic Isolation is a term that refers to selection against traits in organisms that are the product of hybridization. In order to compare the relative contributions of pre-mating and post-zygotic effects to ecological speciation, we measured the fitness and viability of offspring in forced mating trials. We randomly selected mating pairs between allopatric populations (hybrids), and also within each population (in-group). We then compared the viability and fitness of the hybrid offspring against the offspring of in-group matings (Figure 4).

In all trials, we saw little evidence of reduced fitness of hybrids, as compared to offspring from forced matings within populations. We also saw evidence of a small, but significant reduction in viability, on the order of 2-4%.

This result indicates that the architectures of the organisms did not vary sufficiently between populations to produce substantially less-fit or less viable offspring, despite

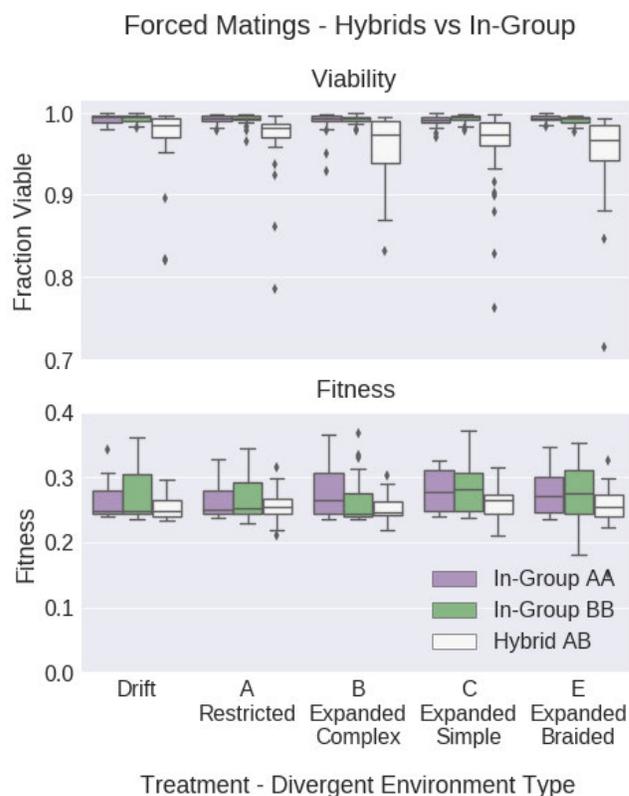


Figure 4: Viability and Fitness of offspring from forced mating trials. Across all treatments, hybrid offspring viability was slightly, but significantly reduced by 2-4%, as compared to in-group forced matings (One-Way ANOVA $F(2,87) = 8.78, 16.15, 13.41, 8.19, \text{ and } 15.43$ respectively, $p < 0.001$). Hybrid fitness, however, was not significantly reduced in most treatments, except for Treatment B, Hybrid vs In-Group AA (Wilcoxon Rank Sum Test: $Z = -2.56, p < 0.05$).

varying sufficiently to produce variation in selected traits and choosiness.

Conclusion and Future Directions

We have shown that sexual selection can have a strong influence on a population's tendency to speciate, acting rapidly in relatively short time-frames, and creating pre-mating isolation well before post-zygotic incompatibilities emerge to cement the status of new species.

Despite finding little evidence for post-zygotic isolation after allopatry, there is little doubt that after long enough periods of time, divergent adaptation, or even pure drift can result in genetic incompatibility between populations (Slatkin, 1987). In the short term, however, while we saw a dramatic reduction in gene-flow between our divided populations, gene-flow was not stopped entirely. In fact, very little

gene-flow is required for populations to erase their differences (Slatkin, 1985). Therefore, questions of how incipient speciation is completed remain open.

One possibility is that the production of unfit hybrids selects indirectly for discrimination against heterospecifics. This process is called reinforcement. Reinforcement, however, is controversial (Bank et al., 2012; Abbott et al., 2013). Models of reinforcement predict that selection will be more effective in sympatry, where incipient species are in more frequent contact. However, as heterospecific discrimination improves, selective pressure for this kind of discrimination decreases. Thus, it is unclear whether reinforcement can actually complete the process of speciation, or if it will instead cause discrimination traits to balance at some sub-speciation level. More research is required to address these questions, and others of how drift and directional selection interact with reinforcement. These interactions may provide a clue to solving these puzzles.

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References

- Abbott, R., Albach, D., Ansell, S., Arntzen, J. W., Baird, S. J., Bierne, N., Boughman, J., Brelsford, A., Buerkle, C. A., Buggs, R., and others (2013). Hybridization and speciation. *Journal of Evolutionary Biology*, 26(2):229–246.
- Anderson, J. L., Morran, L. T., and Phillips, P. C. (2010). Outcrossing and the Maintenance of Males within *C. elegans* Populations. *Journal of Heredity*, page esq003.
- Bank, C., Hermisson, J., and Kirkpatrick, M. (2012). Can reinforcement complete speciation? *Evolution*, 66(1):229–239.
- Canino-Koning, R., Ofria, C., and Wisner, M. J. (2016). The Evolution of Evolvability: Changing Environments Promote Rapid Adaptation in Digital Organisms. In *Proceedings of the Artificial Life Conference 2016*.
- Civetta, A. and Singh, R. S. (1998). Sex and speciation: genetic architecture and evolutionary potential of sexual versus nonsexual traits in the sibling species of the *Drosophila melanogaster* complex. *Evolution*, pages 1080–1092.
- Darwin, C. and Wallace, A. (1858). On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. *Journal of the proceedings of the Linnean Society of London. Zoology*, 3(9):45–62.
- Dunn, O. J. (1961). Multiple comparisons among means. *Journal of the American Statistical Association*, 56(293):52–64.
- Falk, J. J., Parent, C. E., Agashe*, D., and Bolnick, D. I. (2012). Drift and selection entwined: asymmetric reproductive isolation in an experimental niche shift. *Evolutionary Ecology Research*, 14(4):403–423.
- Fay, M. P. and Proschan, M. A. (2010). Wilcoxon-Mann-Whitney or t-test? On assumptions for hypothesis tests and multiple interpretations of decision rules. *Statistics surveys*, 4:1.
- Fisher, R. A. (1930). *The genetical theory of natural selection*. Clarendon Press, Oxford.
- Fricke, C., Andersson, C., and Arnqvist, G. (2010). Natural selection hampers divergence of reproductive traits in a seed beetle. *Journal of evolutionary biology*, 23(9):1857–1867.
- Hendry, A. P., NOSIL, P., and RIESEBERG, L. H. (2007). The speed of ecological speciation. *Functional ecology*, 21(3):455–464.
- Klemetsen, A. (2010). The Charr Problem Revisited: Exceptional Phenotypic Plasticity Promotes Ecological Speciation in Postglacial Lakes. *Freshwater Reviews*, 3(1):49–74.
- Kraaijeveld, K., Kraaijeveld-Smit, F. J., and Maan, M. E. (2011). Sexual selection and speciation: the comparative evidence revisited. *Biological Reviews*, 86(2):367–377.
- Kwan, L. and Rundle, H. D. (2010). Adaptation to Desiccation Fails to Generate Pre- and Postmating Isolation in Replicate *Drosophila Melanogaster* Laboratory Populations. *Evolution*, 64(3):710–723.
- Lande, R. (1981). Models of Speciation by Sexual Selection on Polygenic Traits. *Proceedings of the National Academy of Sciences of the United States of America*, 78(6):3721–3725.
- Lenski, R. E., Ofria, C., Pennock, R. T., and Adami, C. (2003). The evolutionary origin of complex features. *Nature*, 423(6936):139–44.
- Lenski, R. E., Rose, M. R., Simpson, S. C., and Tadler, S. C. (1991). Long-term experimental evolution in *Escherichia coli*. I. Adaptation and divergence during 2,000 generations. *The American Naturalist*, pages 1315–1341.
- Leu, J.-Y. and Murray, A. W. (2006). Experimental evolution of mating discrimination in budding yeast. *Current Biology*, 16(3):280–286.
- McKinley, P., Cheng, B., Ofria, C., Knoester, D., Beckmann, B., and Goldsby, H. (2008). Harnessing Digital Evolution. *Computer*, 41(1):54–63.

- Ofria, C. and Adami, C. (2002). Evolution of genetic organization in digital organisms. In *Evolution as Computation*, pages 296–313. Springer.
- Panhuis, T. M., Butlin, R., Zuk, M., and Tregenza, T. (2001). Sexual selection and speciation. *Trends in Ecology & Evolution*, 16(7):364–371.
- Pitchers, W., Wolf, J. B., Tregenza, T., Hunt, J., and Dworkin, I. (2014). Evolutionary rates for multivariate traits: the role of selection and genetic variation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1649).
- Ritchie, M. G. (2007). Sexual selection and speciation. *Annu. Rev. Ecol. Evol. Syst.*, 38:79–102.
- Ryan, F. J. (1953). Evolution observed. *Scientific American*, 189:78–82.
- Siegal, M. L. and Leu, J.-Y. (2014). On the Nature and Evolutionary Impact of Phenotypic Robustness Mechanisms. *Annual review of ecology, evolution, and systematics*, 45:496–517.
- Slatkin, M. (1985). Gene Flow in Natural Populations. *Annual Review of Ecology and Systematics*, 16:393–430.
- Slatkin, M. (1987). Gene flow and the geographic structure of natural populations. *Science*, 236:787–793.
- Stearns, S. C., Ackermann, M., Doebeli, M., and Kaiser, M. (2000). Experimental evolution of aging, growth, and reproduction in fruitflies. *Proceedings of the National Academy of Sciences*, 97(7):3309–3313.
- West-Eberhard, M. J. (1983). Sexual Selection, Social Competition, and Speciation. *The Quarterly Review of Biology*, 58(2):155–183.