Modeling transitions from biparental to uniparental reproduction in tardigrades

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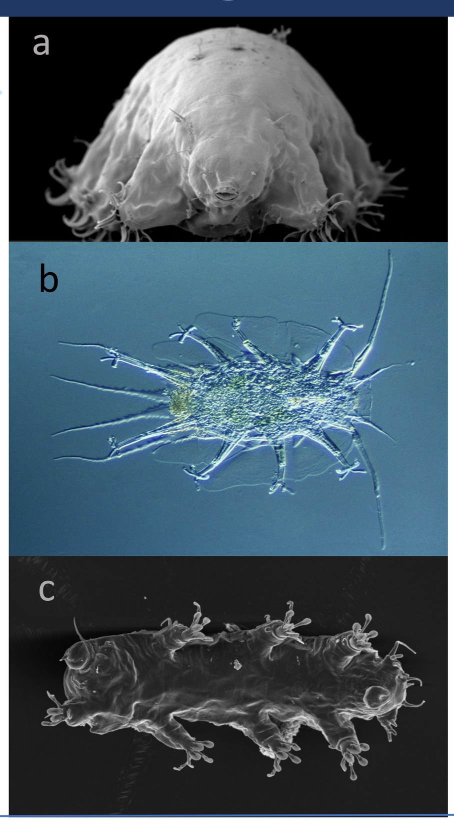
Abstract: Many species of wind-dispersing microscopic animals, such as rotifers, nematodes, and tardigrades, have evolved from biparental ancestors to reproduce uniparentally. Uniparental reproduction is advantageous during dispersal because a lone individual can reproduce in a new environment without needing a mate. Uniparental reproduction has evolved independently several times in these taxa, with different mechanisms resulting in distinct allele inheritance patterns. Our research explores the evolutionary consequences of different mechanisms of uniparental reproduction in terms of colonization success. We contrasted mitotic parthenogenesis (production of clonal female offspring without fertilization) and hermaphroditism (individuals carry both male and female gametes, enabling self-fertilization). Using computational simulations, we tested the hypotheses that 1) parthenogens achieve higher colonization success when the new environment is similar to the ancestral environment because they do not experience inbreeding depression, and 2) hermaphrodites achieve higher colonization success when the new environment differs from the ancestral environment because they produce greater genetic variation which improves their adaptability. We simulated events in which an individual from a source biparental population disperses to a new environment after adopting either parthenogenesis or hermaphroditism, and subsequently either successfully colonizes or faces extinction. Our results confirm the expected costs and benefits of parthenogenesis and hermaphroditism during colonization and help discern probable evolutionary paths from biparental to uniparental reproduction.

Why are semi-terrestrial tardigrades more often parthenogenetic than hermaphroditic?

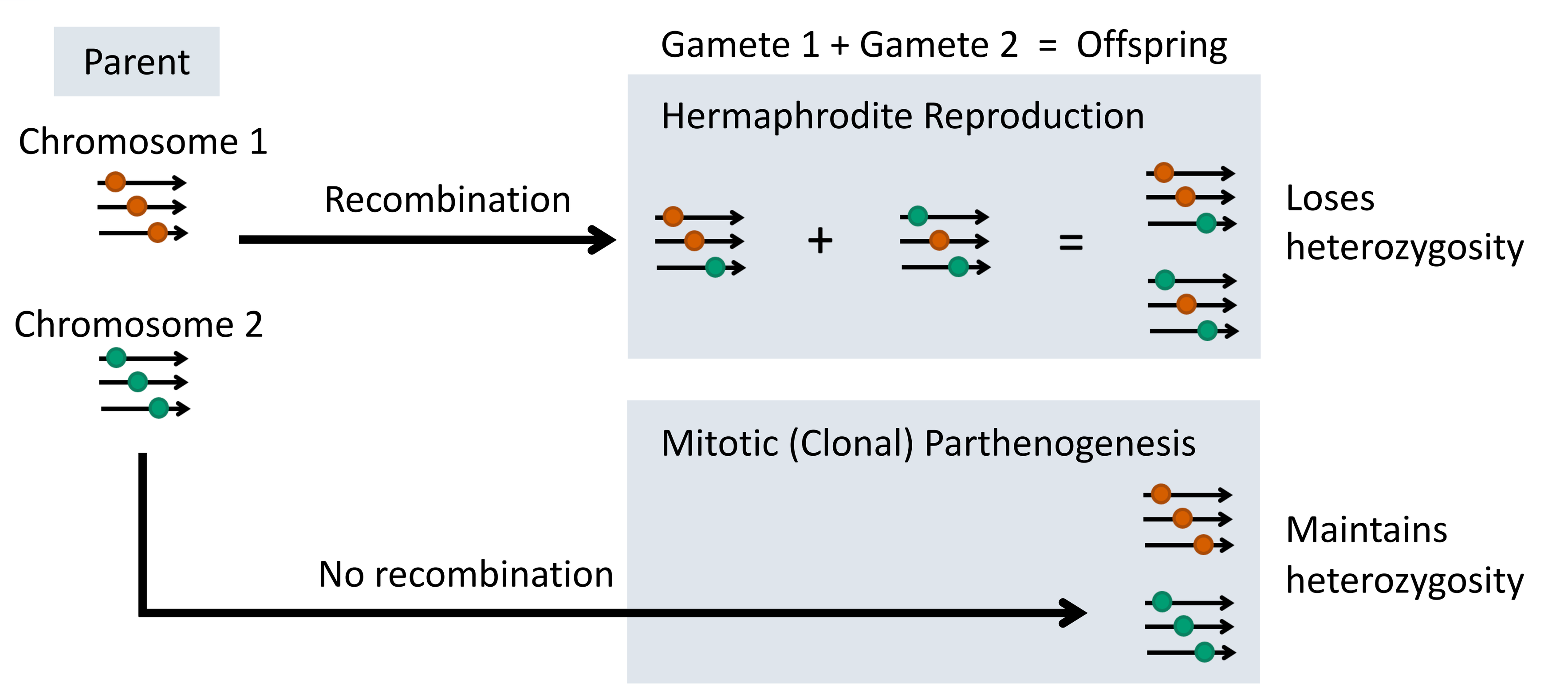
Marine tardigrades

In the marine environment from which the phylum originated, tardigrades nearly always undergo biparental sexual reproduction.[1] Marine tardigrades have dispersed to colonize semi-terrestrial habitats.



Semi-terrestrial tardigrades

Uniparental reproduction allows colonization of new environments by a single individual. Tardigrades in semi-terrestrial habitats primarily use uniparental reproduction, with parthenogenesis far more common than hermaphrodite reproduction.[1]



Hypotheses regarding the colonization of new environments

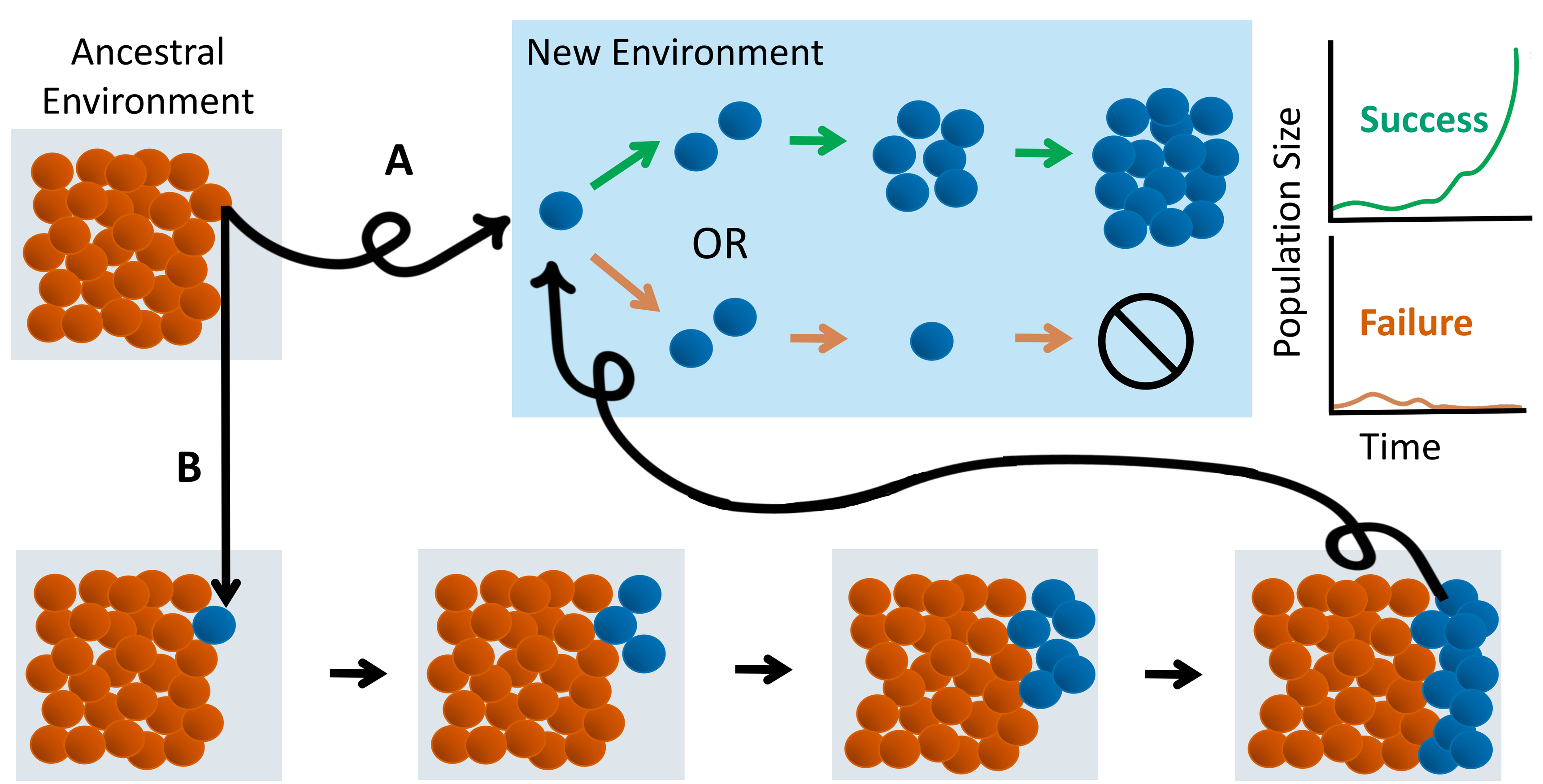
1. Mitotic parthenogens achieve higher colonization success when the new environment is similar to the ancestral environment because they do not experience inbreeding depression.
2. Hermaphrodites achieve higher colonization success when the new environment is different from the ancestral environment because recombination creates genetic variation.[2]

Simulate colonization by dispersing uniparental individuals from ancestral sexual populations

We adapted an existing *haploid* gene regulatory network model[3,4] to represent individuals as *diploid* gene regulatory networks.

Experiment A: An individual using uniparental reproduction disperses from an ancestral sexual population to a new environment & attempts colonization.

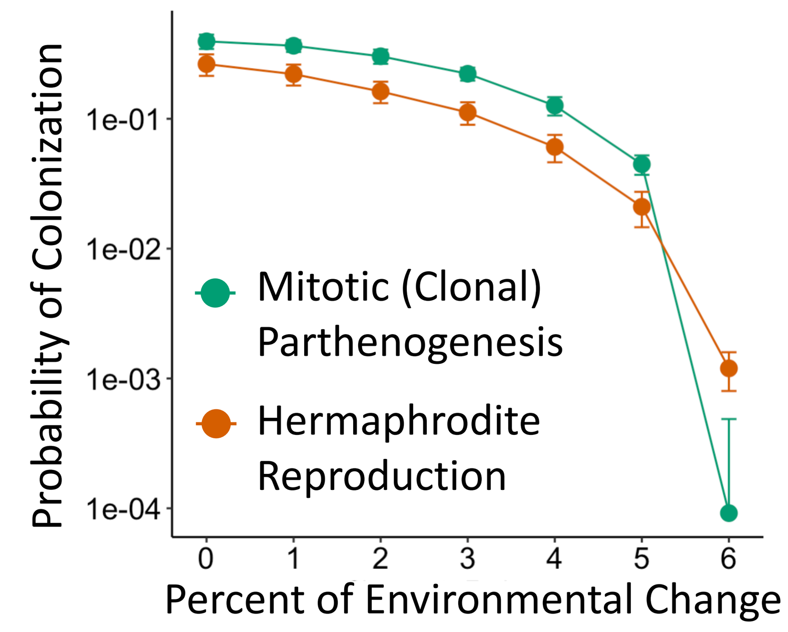
Experiment B: An individual using uniparental reproduction gives rise to a subpopulation in the ancestral environment prior to dispersal & colonization.



Parthenogens colonize more successfully than hermaphrodites unless inbreeding depression is purged or environmental change is substantial.

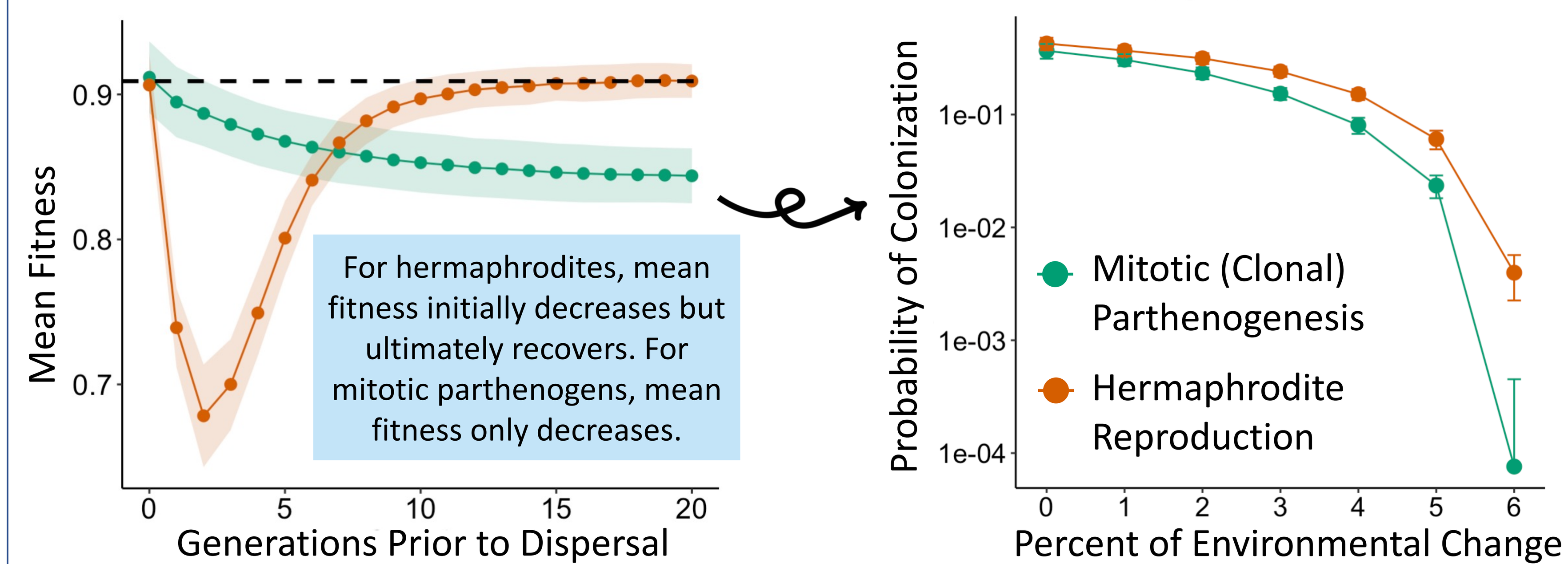
Primary results

Experiment A: Hermaphrodites have lower colonization success than mitotic parthenogens when the new environment is similar to the ancestral environment. Hermaphrodites have higher colonization success than mitotic parthenogens when the new environment is substantially different from the ancestral environment.



Testing hypothesis 1

Experiment B: When inbreeding depression is purged in a subpopulation prior to dispersal (left), hermaphrodites have higher colonization success than mitotic parthenogens even when the new environment is similar to the ancestral environment (right).



Testing hypothesis 2

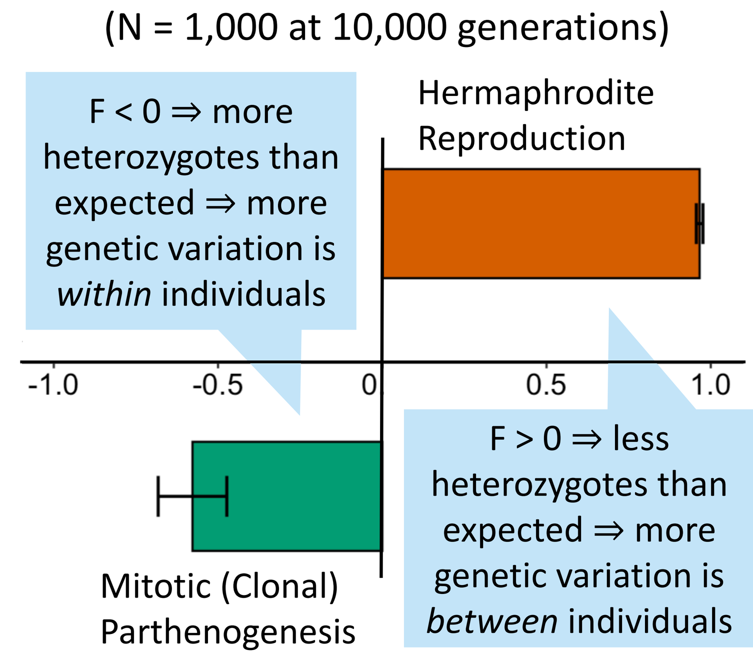
F measures how much the observed proportion of heterozygotes (H_O) differs from the expected proportion of heterozygotes based on allele frequencies (H_E).

$$F = \frac{H_E - H_O}{H_E}$$

Higher between-individual genetic variation (F > 0) in hermaphrodites may increase adaptability compared to mitotic parthenogens (F < 0) which is beneficial under substantial environmental change.

F of Evolved Populations

(N = 1,000 at 10,000 generations)



What are the next steps to confirm the evolutionary processes favoring certain modes?

1. Measure rate of fitness increase in the new environment as a proxy for adaptability
   - Expectation: Hermaphrodites have a higher rate of fitness increase than mitotic parthenogens because of higher between-individual genetic variation.
2. Explore forms of meiotic parthenogenesis with small amounts of recombination
   - Meiotic parthenogens may have higher colonization success than mitotic parthenogens when the environment changes substantially.

 References: [1]Bertolani *Zoologischer Anzeiger-A Journal of Comparative Zoology* (2001). [2]Hill & Robertson *Genetics Research* (1966). [3]Wagner *Evolution* (1996). [4]Whitlock et al. *Genetics* (2016). **Acknowledgements:** Funded by a Summer Undergraduate Research Fellowship from the OUR at UNC-CH awarded to BB, National Science Foundation grant DEB-2014943 to CLB, and a National Institute of General Medical Sciences training grant fellowship to ACS under award 5T32GM135128.