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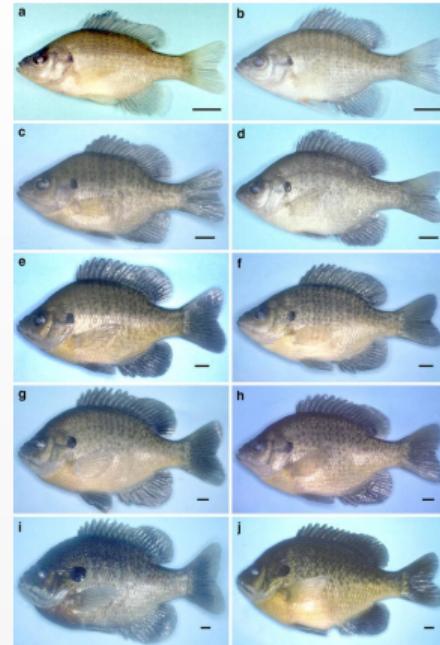
Variation in resource quality causes
maintenance of individual variation in a competitive trait
MPDEE 2024

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joint work with Klaus Reinhold (Bielefeld) and David W. Kikuchi (Oregon State)

Individual variation

- Evolution does not necessarily lead to identical individuals.
- Individual variation is ubiquitous in many populations.
- This includes **genetic variation**.
- Potential causes: temporal/spatial environmental variability, negative frequency-dependent selection, ...



Bluegill size differences¹

¹ (Yokogawa, K.: *Ichthyological Research* 60.1 [2012])

Individual variation in competitive traits

- Traits determining intraspecific competitiveness often vary within populations.
- Examples: armaments, body size, sensory capabilities to detect food, ...
- **Investment into competitiveness typically bears a cost.**
- Trade off between ability to attain resources and resource investment into competitive features.



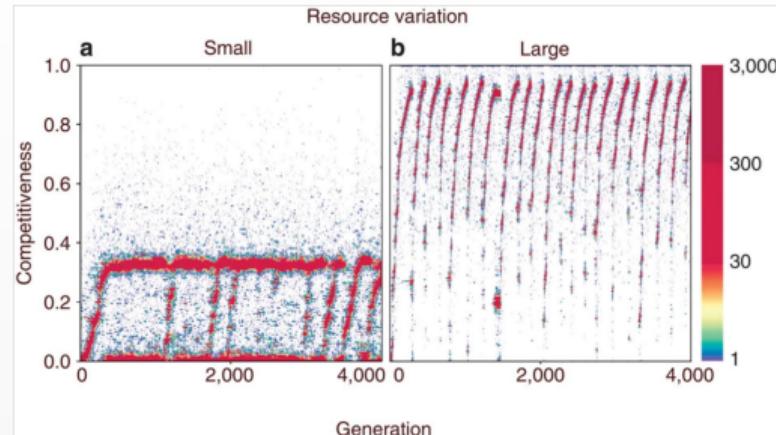
Source: Wikimedia Commons

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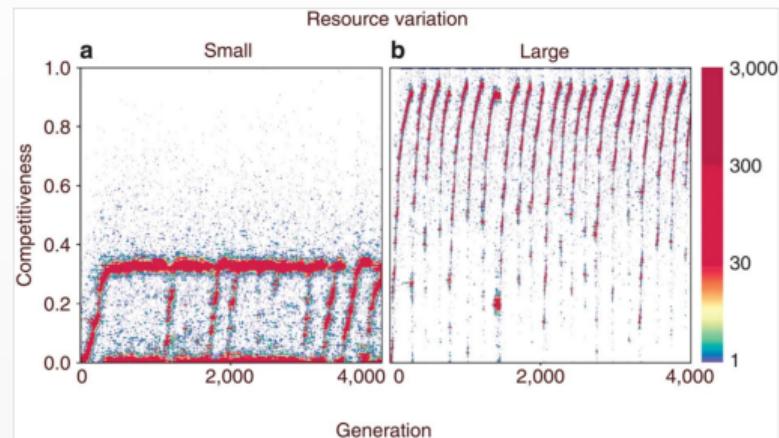


Source: Wikimedia Commons

(Baldauf, S. A., Engqvist, L. and Weissing, F. J.: *Nat. Commun.* 5.1 [2014])

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- Notable exception: Assuming a continuous competitive trait in a population competing for two different resource quality levels found either dimorphisms or repeated cycles of “arms races” depending on the difference between the two resource quality levels.²
- What if resource qualities also vary continuously?



Source: Wikimedia Commons

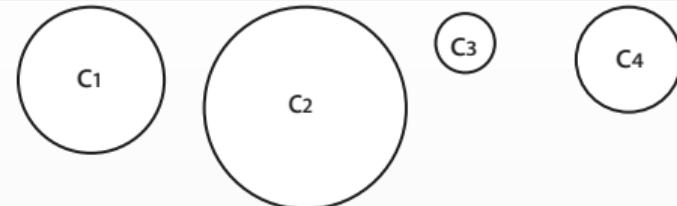
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Individual based model



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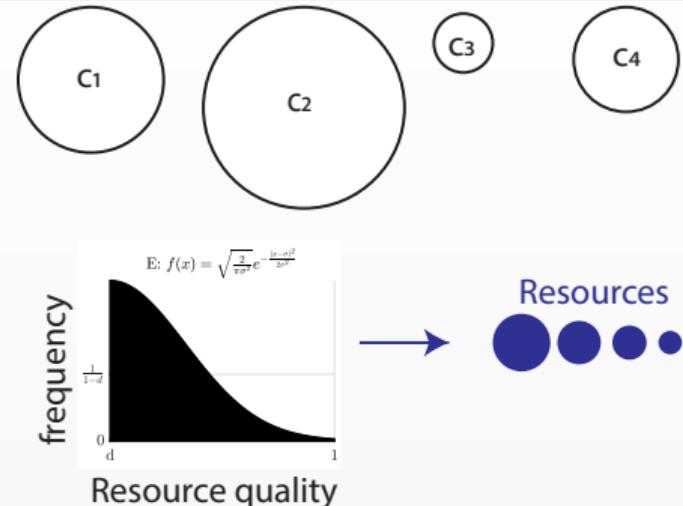
Individual based model



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- Individual $i \in \{1, \dots, N\}$ has competitive trait $c_i \geq 0$.

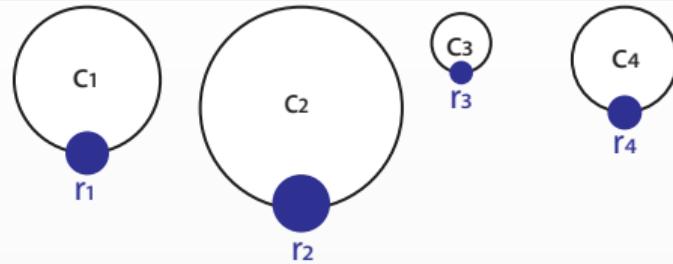
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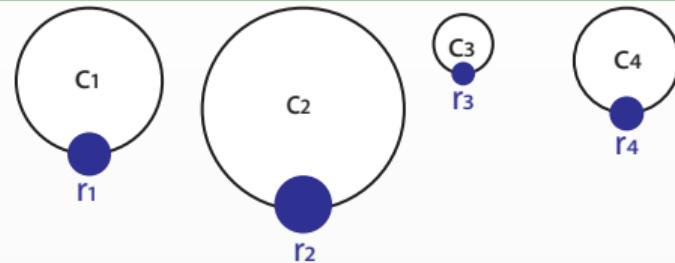
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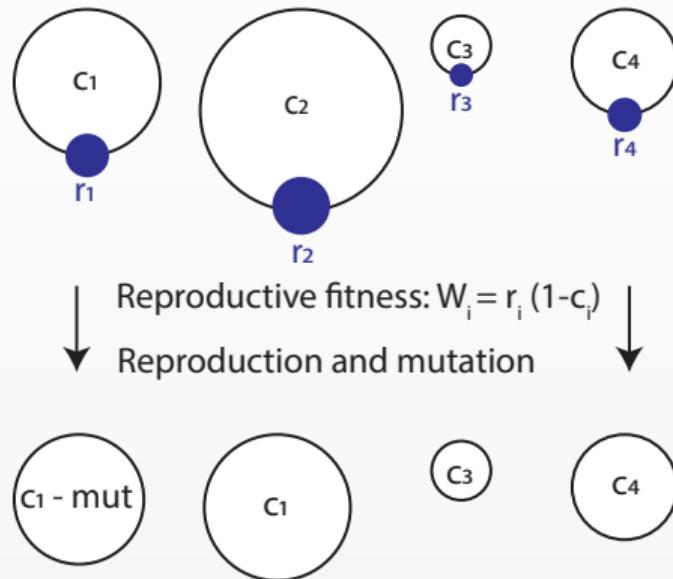
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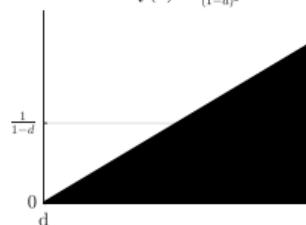
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- Next generation is created through draw with replacements with weights W_i and mutations.



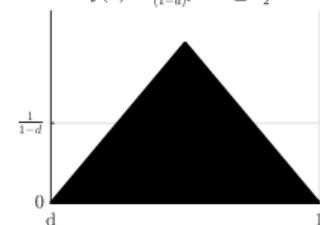
Resource distributions

- A: linearly increasing
- B: linearly increasing and decreasing
- C: uniform
- D: linearly decreasing
- E: half-normal
- F: power law

A: $f(x) = \frac{2(x-d)}{(1-d)^2}$



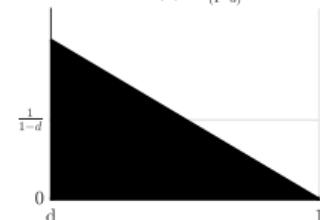
B: $f(x) = \frac{4(x-d)}{(1-d)^2}$ if $x \leq \frac{1+d}{2}$
 $f(x) = \frac{4(1-x)}{(1-d)^2}$ if $x \geq \frac{1+d}{2}$



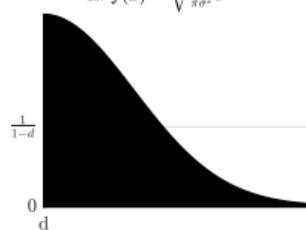
C: $f(x) = \frac{1}{1-d}$



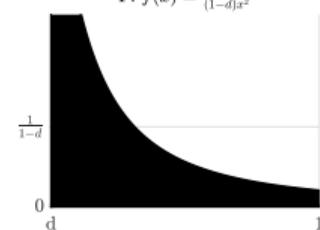
D: $f(x) = \frac{2(1-x)}{(1-d)^2}$



E: $f(x) = \sqrt{\frac{2}{\pi\sigma^2}} e^{-\frac{(x-\mu)^2}{2\sigma^2}}$

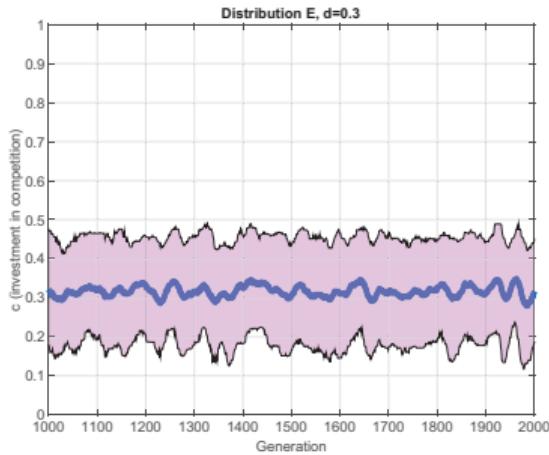
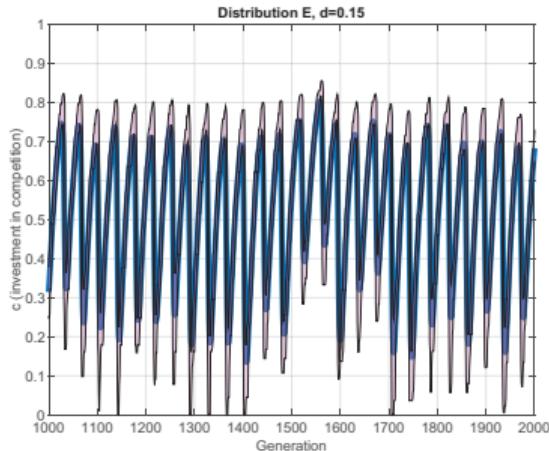


F: $f(x) = \frac{d}{(1-d)x^2}$



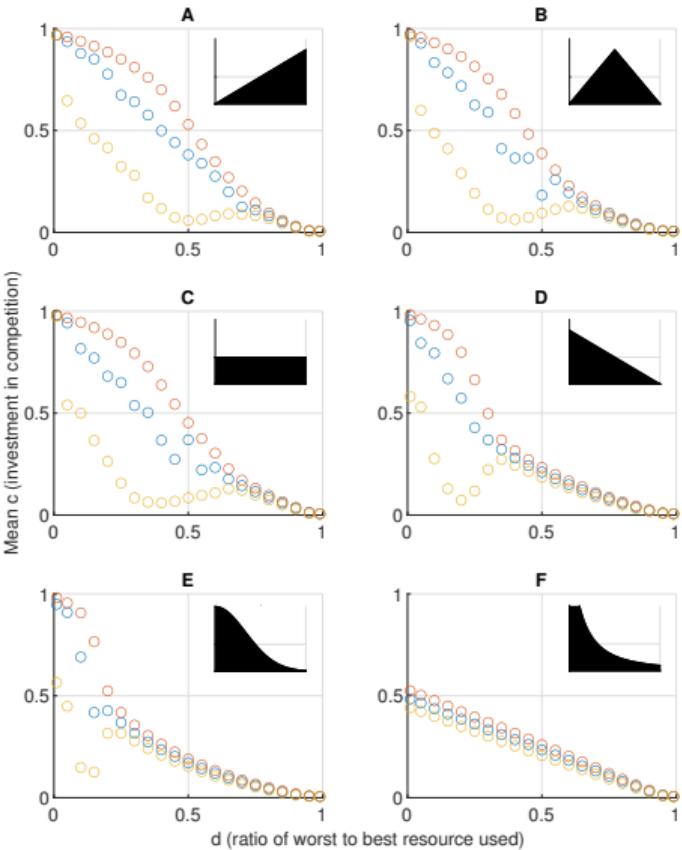
Arms races vs. stable polymorphisms

- Dynamics either represent **arms races** or **stable polymorphisms**.
- Arms race: mean competitive trait oscillates with little individual variation at a time.
If all individuals have $c = c^*$, then $c = c^* + \varepsilon > c^*$ has higher fitness.
If c^* is high, low competitive traits can invade; in particular, $c_1 = 0$ (fitness $W = (1 - c_1)d = d$) has larger fitness than $c_2 > 1 - d$ because $W = (1 - c_2)r < dr \leq d$.
- Stable polymorphism: mean competitive trait remains constant over time; large individual variation at all times.



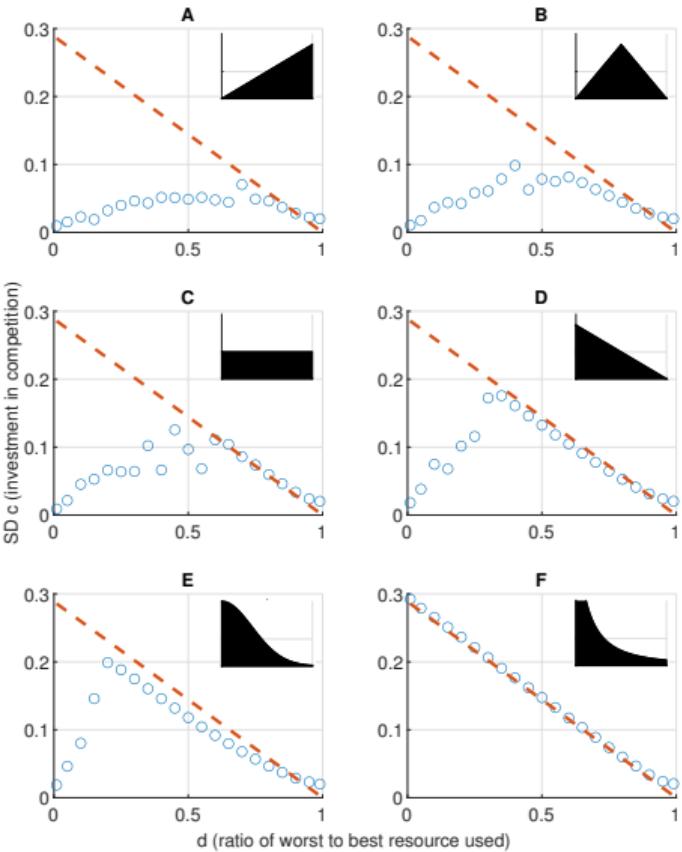
Worst-to-best resource ratio

- The ratio d of the worst to the best resource determines mean investment into competition.
- Arms races occur when d is small.
- No arms races for power law distribution.
- Stable mean trait values occur when the ratio d of the worst to the best resource is small.
- The threshold $d = d^*$ depends on the resource distribution.



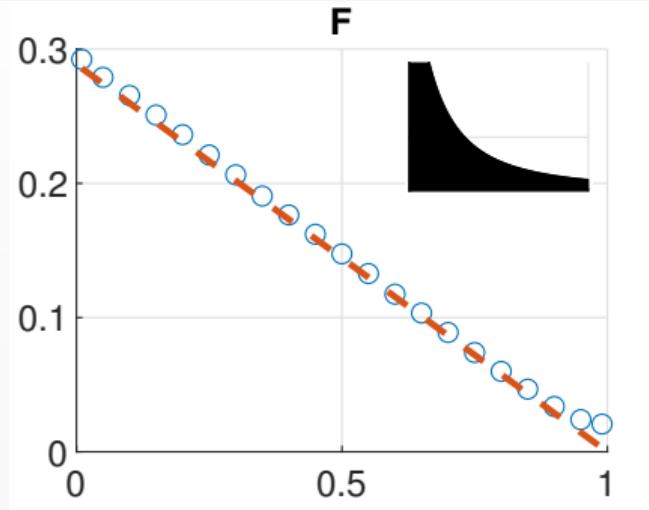
Worst-to-best resource ratio

- Little individual variation occurs during arms races.
- Stable mean trait values are always associated with stable polymorphisms.
- Individual variation is close to maximum (uniform distribution with $0 \leq c \leq 1 - d$).



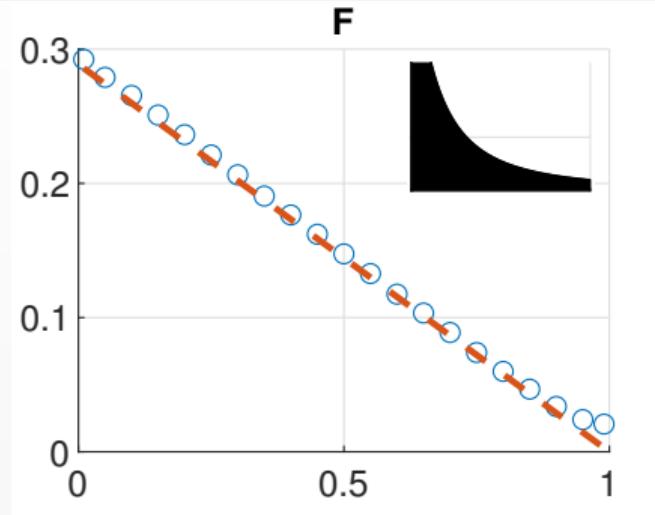
Special case: power law

- Can show analytically that the power law with pdf $g(r) = \frac{d}{(1-d)r^2}$ leads to uniform trait distribution.



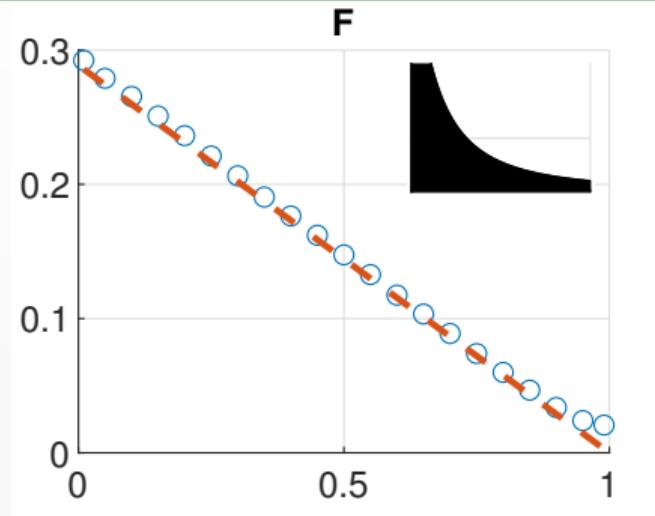
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- look for trait distribution in which all values $0 \leq c \leq 1 - d$ attain equal fitness
 $W = (1 - c)r(c) = d \Leftrightarrow r(c) = \frac{d}{1-c}.$



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 $W = (1 - c)r(c) = d \Leftrightarrow r(c) = \frac{d}{1-c}.$
- Hierarchical resource assignment means
 $P(r < r^*) = P(c < c^*), \text{ where } r^* = \frac{d}{1-c^*}.$

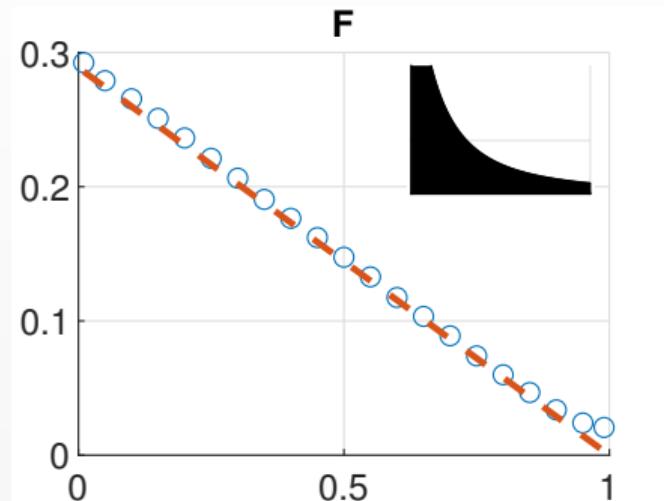


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Therefore, the cdf of the trait distribution is

$$P(c < c^*) = P(r < r^*) = \frac{r^* - d}{(1 - d)r^*} = \frac{c^*}{1 - d}.$$

⇒ uniform distribution.



Conclusions

- Continuous individual variation in a competitive trait is a consequence of intraspecific competition for resources with continuously varying quality.
- The ratio between worst and best quality resources determines (i) mean investment into competition, and (ii) whether arms races with little individual variation or stable polymorphisms occur.
- The distribution of resource quality is important.
- Resource distributions with more low-quality resources lead to stable polymorphisms in more cases.

References

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- [1] Reinhold, K., Eigentler, L. and Kikuchi, D. W.: 'Evolution of individual variation in a competitive trait: a theoretical analysis'. *Journal of Evolutionary Biology* (2024).