"The evolution of germ-soma specialization under different genetic and environmental effects"

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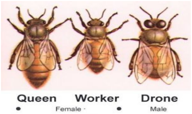
Division of labor

- Germ-soma specialization in Volvocales, cyanobacteria, and hydrozoans;

- Specialization in carbon fixation and nitrogen fixation in cyanobacteria;

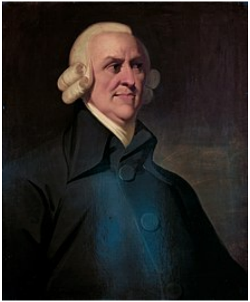
- Casts in social insects;

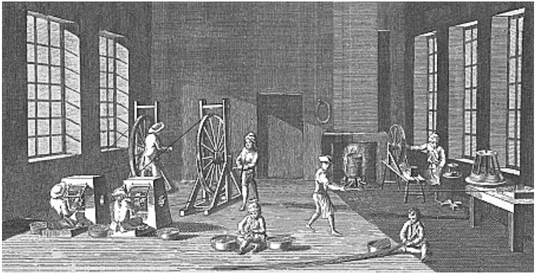


- Sexual division of labor in small hunter-gatherer groups;

- Division of labor in complex societies.

Division of labor in economic theory





Germ-soma specialization

Germ-soma specialization Reproductive altruism → Biological complexity

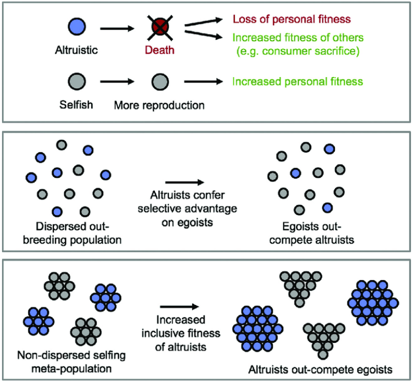
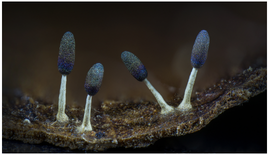


Figure: Lohr, J.N., Galimov, E.R. and Gems, D., 2019. Does senescence promote fitness in Caenorhabditis elegans by causing death?. Ageing Research Reviews, 50, pp.58-71.

Effects of environmental conditions on germ-soma specialization. Examples:

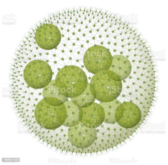
- Effects of temperature and oxygen concentration on slime molds

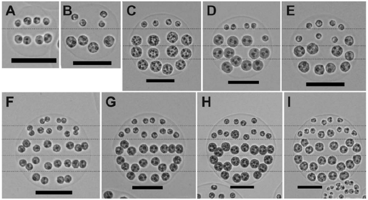


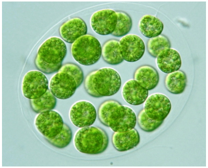
- Effects of water stress and cold on Volvocales in general
- Effects of mixed and still environment on Pleodorina starrii colonies

Effects of microenvironmental conditions on germ-soma specialization. Examples:

- Oxygen and nutrient gradients in biofilms;
- Iron gradients in S.coelicolor colonies;
- Examples in volvocaleans green algae: Volvox (left), Pleodorina (middle), Eudorina (right)[1]:







[1] Pictures from:

- https://www.istockphoto.com/vector/volvox-gm959301582-261956197
- Herron, M.D., Ghimire, S., Vinikoor, C.R. and Michod, R.E., 2014. Fitness trade-offs and developmental constraints in the evolution of soma: an experimental study in a volvocine alga. Evolutionary ecology research, 16(3), p.203.
- https://alchetron.com/Eudorina

Mathematical models of the emergence of germ-soma specialization:

- Trade-offs between reproductive and somatic functions (Michod, 2006, Leslie et al., 2017),
- group size (Michod, 2006),
- genetic relatedness (Cooper and West, 2018),
- developmental plasticity (Gavrilets, 2010),
- positional effects (Reuffler and Wagner, 2012), ,
- topological constraints (Yanni et al., 2020),
- resource constraint, positional effects, and the trade-off curvature (Tverskoi et al., 2018)

The model

We examine effects of environmental factors, positional effects and the trade-off between cell activity and fecundity on the evolution of germ-soma specialization in cell colonies.

Environmental effects in the model:

- At a between-colony level (resource-based competition)
- At a within-colony level (different microenvironmental effects on gene expressions)

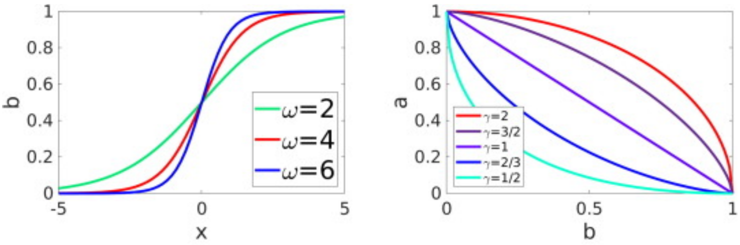
The model: a general outline

- A finite population of colonies each composed by S asexually reproducing haploid cells,
- gene effects are affected by variation in microenvironment experienced by individual cells within a colony,
- colonies compete for resources,
- colonies surviving to the stage of reproduction disintegrate and the released cells start new daughter-colonies,
- mutation occurs during cell division.

The model: cell genotype and phenotype

- All cells within a colony are genetically identical. The cell's genotype is $g = (g_1, .., g_G), g \in [0,1]^G$.
- These genes control a cell's activity a and fecundity b, $a, b \in [0,1]$.
- We define the i-th gene's effect on fecundity as $x_i = e_i g_i$, where e_i specifies microenvironmental effects. Microenvironment effects e_i may differ between different cells of the same colony.

The model: cell genotype and phenotype



(a) (b)

- We define a cell's fecundity as $b = \frac{1}{1+\exp\left(-\omega\frac{x}{\sqrt{G}}\right)}$, where $x = \sum x_i$ is the cumulative gene effect.
- Fecundity and activity within each cell are traded off: $a = (1 - b^\gamma)^{\frac{1}{\gamma}}$, $\gamma > 0$ controls the shape of the trade-off relation.

Trade-off curvature and colony size

The trade-off function between activity and fecundity is convex-like for large-size colonies, and concave for small-size colonies.

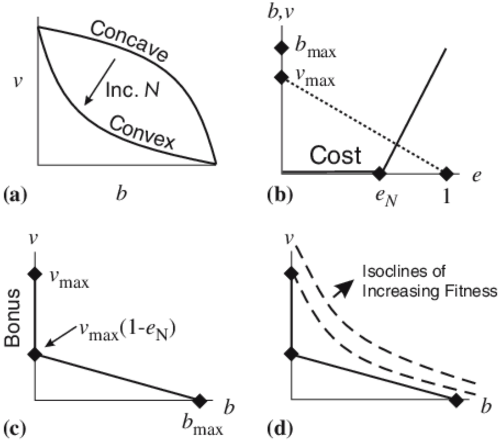
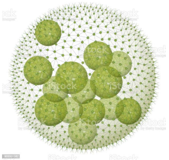


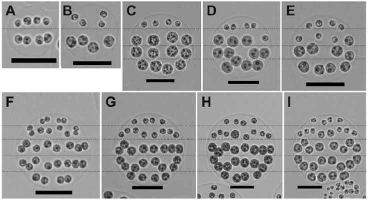
Figure: Michod, R.E., Viossat, Y., Solari, C.A., Hurand, M. and Nedelcu, A.M., 2006. Life-history evolution and the origin of multicellularity. Journal of theoretical Biology, 239(2), pp.257-272.

Cell microenvironment and cell prototypes

Cells can differ in size or position in the colony, which can impact on their gene effect on fecundity.

- In Volvox the *regA* gene $\downarrow$ reproduction in small cells (proto-soma), the *lag* gene $\downarrow$ motility in large cells (proto-germ).
- In *Pleodorina starrii*, cells are divided into tiers arranged from the anterior to the posterior of determined according to the motility direction.[2]





A colony consists of groups of cells experiencing the same $e = (e_1, \ldots, e_G)$, and cells belonging to different groups are characterized by different vectors e. Cells in the same group have the same *prototype*, and cells of different groups have different prototypes (s is the number of prototypes).

[2] Pictures from:

- https://www.istockphoto.com/vector/volvox-gm959301582-261956197
- Herron, M.D., Ghimire, S., Vinikoor, C.R. and Michod, R.E., 2014. Fitness trade-offs and developmental constraints in the evolution of soma: an experimental study in a volvocine alga. Evolutionary ecology research, 16(3), p.203.

Cell microenvironment and cell prototypes

Two ways of specifying microenvironmental effects e_{mi} $(m = 1, .., s; i = 1, .., G)$:

- **Random microenvironmental effects**. $e_{m,i}$ is drawn randomly and independently from a uniform distribution on $[-1, 1]$.
- **Microenvironmental gradients**, $e_{m,i}$ change according to some gradient along the anterior-posterior axis.
  $|e_{m,i}|$ decreases geometrically at rate r with the distance m from the anterior layer: $e_{m+1,i} = re_{m,i}$ with $|e_{1,i}| = d$, $d > 0$.

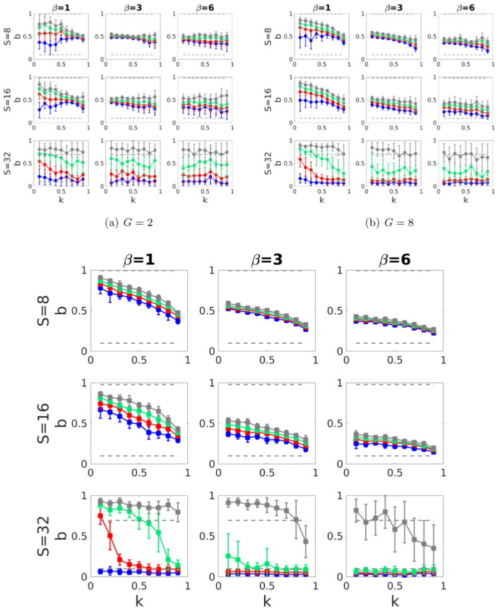
Colony survival

- Colonies compete for a resource $C > 0$. The amount of the resource a colony secures in competition is $R = C \cdot \frac{A^\beta}{\sum A^\beta}$, where $A = \sum_j a_j$, $\beta \geq 1$ is the strength of competition.
- The colony always survives to the stage of reproduction if $R \geq R_0$. If $R < R_0$, the probability of survival is $V = R/R_0$, where $R_0 = (1-k)A + kB$ and $0 < k < 1$ measures the relative cost of fertility.

Other details

- **Reproduction**. Each surviving colony disintegrates into S cells and each cell seeds a new colony with probability b_i. Mutations in an offspring colony genotype g happen with probability μ per gene.
- We define *a cell phenotype* as its fecundity b. Cells of the same prototype have the same phenotype. Cells of different prototypes can have the same phenotype as well. $\rightarrow$ the number of different cell phenotypes $M \leq s$.

Results: random microenvironmental effects



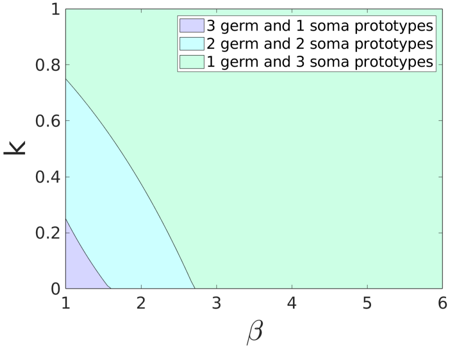
(a) $G = 2$ (b) $G = 8$

(c) $G = 32$

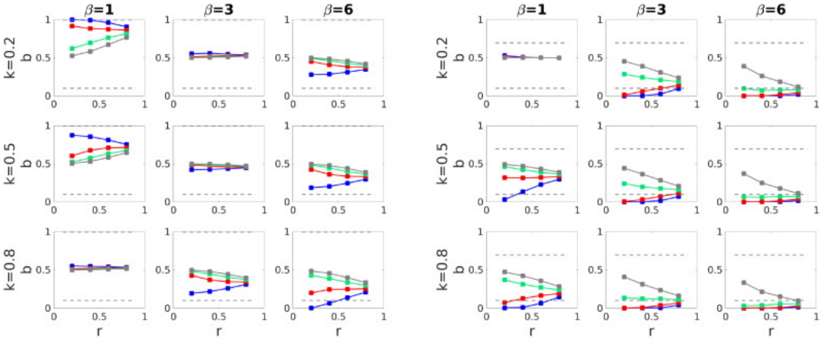
Some analytical results

Analytical approximations (for $G \to \infty$) show that

- In the case of concave trade-offs and random microenvironmental effects, equilibrium cell fecundity b^* can be found as $\frac{k\beta}{1-k} \cdot {b^*}^{\gamma+1} = (1 - \beta {b^*}^{\gamma}) \cdot (1 - {b^*}^{\gamma})^{\frac{1}{\gamma}}$.
- In the case of convex trade-offs, all prototypes or all prototypes except one are specialized.



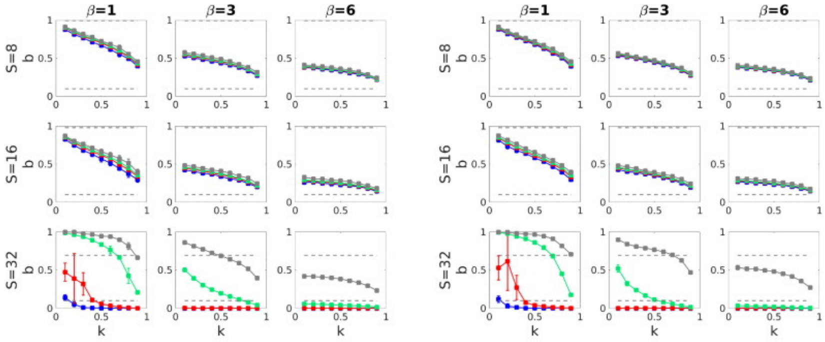
Results: single gradient



(a) $S = 8$ (b) $S = 32$

Cell prototypes are marked in blue, red, green and gray colors respectively along the anterior-posterior axis.

Results: several gradients



(a) $G = 8$ (b) $G = 32$

Prototypes are sorted by increasing fecundity and marked with different colors.

Summary of the results

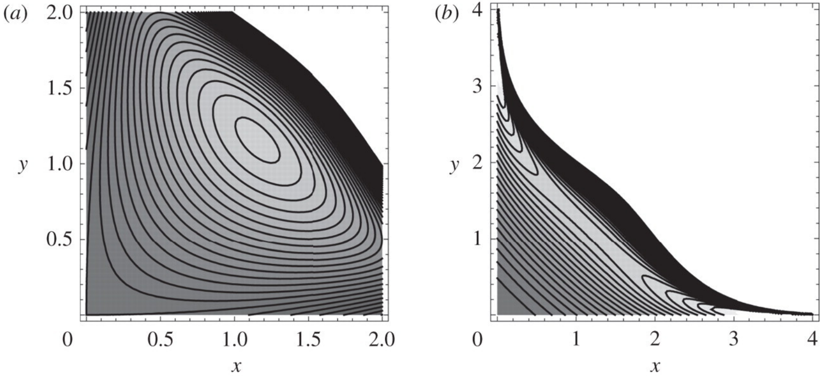
ME	Size	G	Typical patterns of within-colony differentiation	Conditions for coexistence of reproductive and somatic cells
R	S	L	One type of unspecialized cells	-
		S	One or two types of unspecialized cells	-
	L	L	Two types of cells: somatic and reproductive or somatic and unspecialized	All cases except one with large k and β
		S	Three types of cells: somatic, reproductive and unspecialized	Can be observed for all k and β, conditions are determined by random microenvironmental effects
1G	S	S&L	One type of unspecialized cells, or 2 types of cells (somatic and unspecialized or reproductive and unspecialized)	-
	L	- " -	One type of unspecialized cells, or 2 types of cells (somatic and unspecialized or 2 unspecialized) or 3 types of cells (somatic and 2 unspecialized)	-
SG	S	- " -	One type of unspecialized cells	-
	L	- " -	Two types of cells (somatic and reproductive or somatic and unspecialized) or three types of cells (somatic, reproductive and unspecialized)	β is not large and k is not large

Some conclusions

- Specialization can evolve even if the curvature of the trade-off is concave. Incomplete specialization or even colonies composed only by unspecialized cells can be observed in the case of a convex trade-off.
- The type and extent of variation in within-colony microenvironment and, in the case of random microenvironment, the number of genes involved, are key factors shaping the model dynamics

Some conclusions

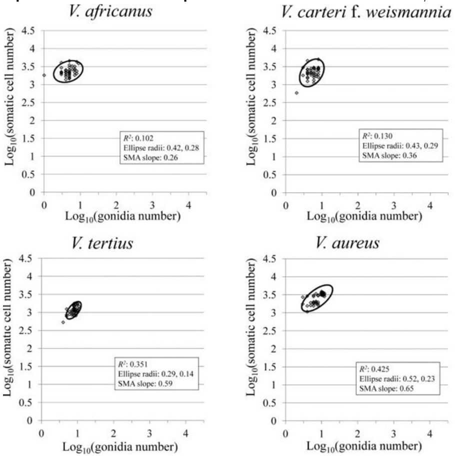
Increasing $s \rightarrow \uparrow W$. This happens because $\uparrow s \rightarrow \uparrow$ in the dimensionality of phenotype space. This generates a fitness landscape with a new fitness maximum, in which colony phenotypes that are fitness optimal for smaller number of gradients become fitness saddle points.



Pictures from: Ispolatov, I., Ackermann, M. and Doebeli, M., 2012. Division of labour and the evolution of multicellularity. Proceedings of the Royal Society B: Biological Sciences, 279(1734), pp.1768-1776.

Some conclusions

The share of reproductive cells in large colonies is smaller than that of somatic cells, with the exceptions of some special cases with small β and k.



Pictures from: Shelton, D.E., Desnitskiy, A.G. and Michod, R.E., 2012. Distributions of reproductive and somatic cell numbers in diverse Volvox (Chlorophyta) species. Evolutionary ecology research, 14, p.707.

Thank you for your attention!