The Unicorn Equation: Conceptual unification of ecology, evolution, and ecosystem function: TESTING

BES Tuesday seminars this autumn

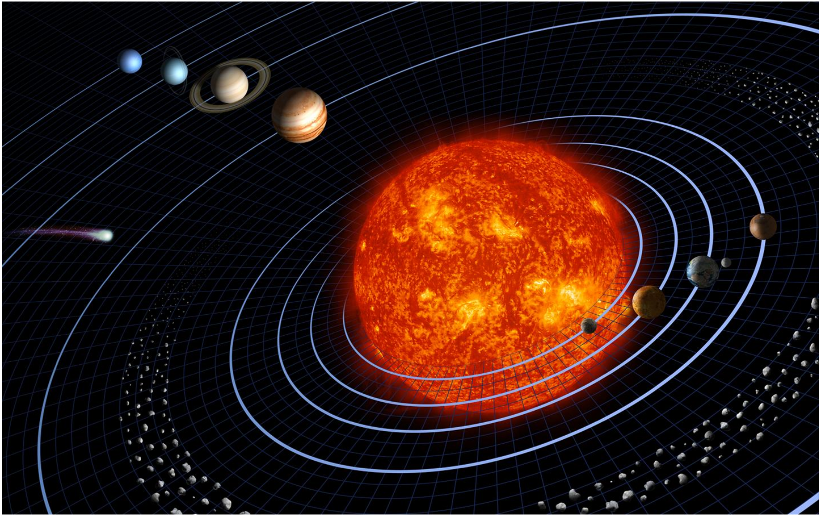
TEG: LT W1 from 13:00-14:00 (until 26 NOV)

Date	Speaker	Date	Speaker
24 SEP	Heather Anderson	05 NOV	Reuben Nowell
01 OCT	**Open**	12 NOV	Ruth Wright
08 OCT	Matt Tinsley	19 NOV	Zarah Pattison
15 OCT	Carmen Carmona	26 NOV	Kirsty Park
22 OCT	Mahtab Yaghouti	03 DEC	Emily Waddell
29 OCT	Ponsarut Boonchuay	10 DEC	Colin Bull

Why people do science, particularly biology

[1] Image: Gillette, B. 1972. Public Domain

Unification of celestial and terrestrial motion



[1] Image: Smith, H and L Generosa (2006). Public Domain

Big questions in biology

Big questions in biology

Prof Brent Danielson (left)

Call for proposals: joint sDiv-CESAB

THE FRB IN ACTION

Home > The FRB in action > The calls > Joint Call CESAB- sDiv SYNERGY: Coexistence and stability in high-diversity communities

PROPOSAL DEADLINE 4TH SEPTEMBER 2019

Joint Call CESAB- sDiv SYNERGY: Coexistence and stability in high-diversity communities

FRB CESAB sDiv synthesis centre of iDiv

CESAB and sDiv are instruments of the French FRB (Foundation for Research on Biodiversity) and German iDiv (German Centre for Integrative Biodiversity Research). These two centers offer to host groups of researchers to work on a better use of existing data, information and knowledge to foster theoretical, and synthetic thinking

USEFUL INFORMATION

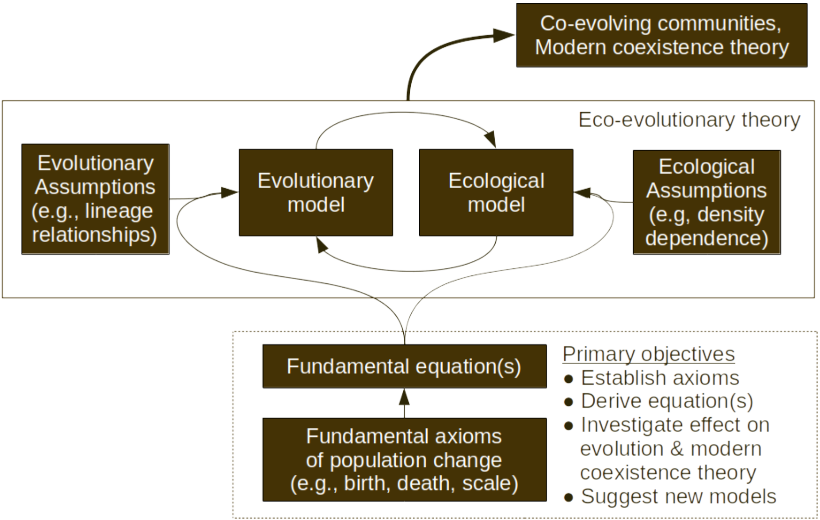
IMPORTANT DATES

- **September 4th 2019**
  Pre-Proposal deadline
- **September 27th 2019**
  Invitation to submit a full-proposal
- **November 15th 2019**
  Full-proposal deadline
- **January 2020**
  Final decision will be made

CONTACT

cesab@fondationbiodiversite.fr

Call for proposals: joint sDiv-CESAB



Conceptual unification of modern coexistence theory and the Price equation

A different role of theory (not doing modelling)

- Framework for making models (meta-modelling)

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$$y_i = \beta_0 + \beta_1 x_i + \epsilon_i$$

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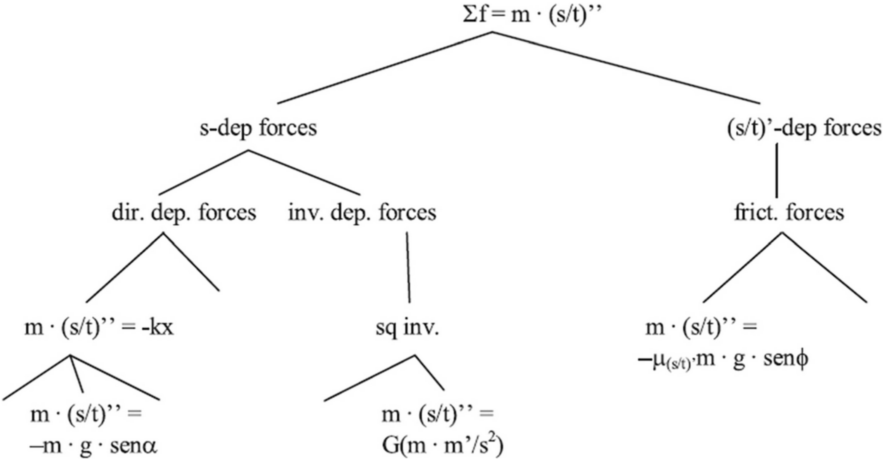
- Framework for making models (meta-modelling)
- Not making assumptions or predictions
- Not the kind of thing we test, e.g.,

$$y_i = \beta_0 + \beta_1 x_i + \epsilon_i$$

- Or Newton's second law, $F = ma$

Newtonian mechanics as a theory net



[1]Luque, VJ, & L Baravalle (2021). The mirror of physics: on how the Price equation can unify evolutionary biology. Synthese, 0123456789.

The fundamental equation of evolution

$$\bar{w}\Delta\bar{z} = Cov\left(w, z\right) + E\left(w\Delta z\right)$$

[1] Price, GR (1970). Selection and covariance. Nature 227:520–521.

[2] Luque, VJ (2017). One equation to rule them all: a philosophical analysis of the Price equation. Biology and Philosophy, 32:1–29.

[3] Lehtonen, J, Okasha, S, & Helanterä, H (2020). Fifty years of the Price equation. Philosophical Transactions of the Royal Society B: Biological Sciences, 375:20190350.

[4] Frank, SA (2012). Natural selection. IV. The Price equation. Journal of Evolutionary Biology, 25, 1002–1019.

[5] Lion, S (2018). From the Price equation to the selection gradient in class-structured populations: a quasi-equilibrium route. Journal of Theoretical Biology, 447, 178–189.

The fundamental equation of evolution

represent $\Delta q_i = q_i' - q_i$ as the change associated with differential survival and reproduction and $\Delta z_i = z_i' - z_i$ as the property value change. Following these definitions, the Price equation expresses the total change in the average property value as $\Delta\bar{z} = \bar{z}' - \bar{z}$. Now we can substitute and derive:

$$\begin{aligned}\Delta\bar{z} &= \bar{z}' - \bar{z}\\ &= \sum q_i' z_i' - \sum q_i z_i\\ &= \sum q_i'(z_i' - z_i) + \sum q_i' z_i - \sum q_i z_i\\ &= \sum q_i'(\Delta z_i) + \sum (\Delta q_i) z_i\end{aligned}$$

Switching the order of the terms and substituting and rearranging:

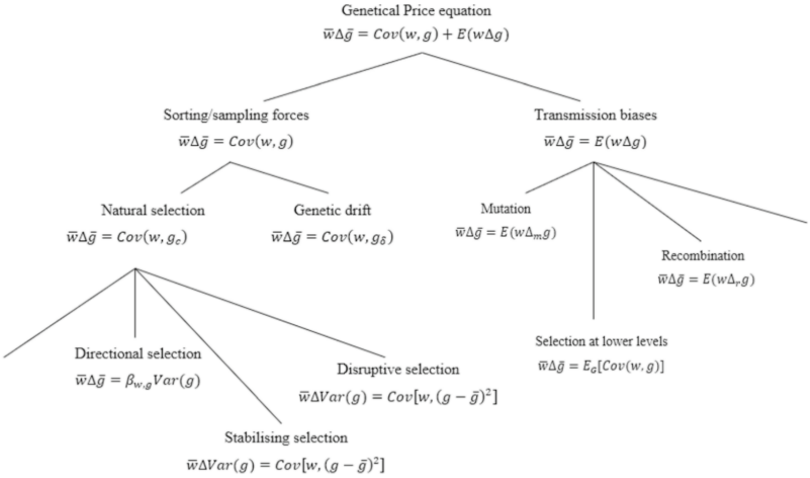
$$\Delta\bar{z} = \sum q_i\left(\frac{w_i}{\bar{w}} - 1\right) z_i + \sum q_i \frac{w_i}{\bar{w}}(\Delta z_i)$$

Applying the standard definitions of covariance and expectation we obtain

$$\bar{w}\Delta\bar{z} = Cov(w, z) + E(w\Delta z) \tag{1}$$

[1] Luque, VJ (2017). One equation to rule them all: a philosophical analysis of the Price equation. Biology and Philosophy, 32:1–29.

The fundamental equation of evolution



[1] Luque, VJ, & L Baravalle (2021). The mirror of physics: on how the Price equation can unify evolutionary biology. Synthese, 0123456789.

Recursive properties of the Price equation

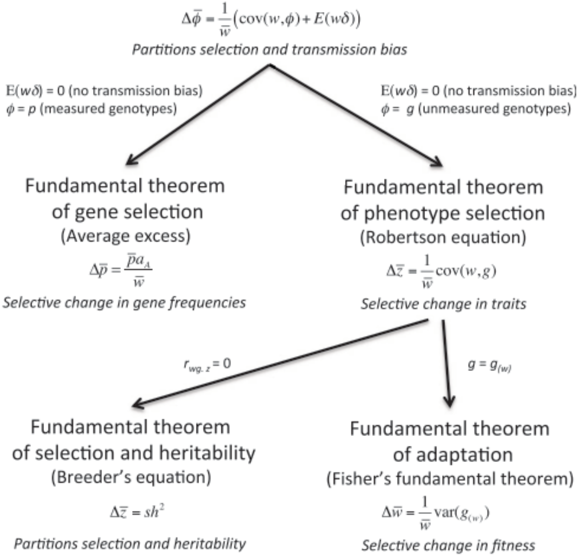
$$\bar{w}\Delta\bar{z} = Cov\left(w, z\right) + E\left(w\Delta z\right)$$

[1] Price, GR (1970). Selection and covariance. Nature 227:520–521.

[2] Kerr, B, & P Godfrey-Smith (2009). Generalization of the price equation for evolutionary change. Evolution, 63:531–536.

[3] Frank, SA (2012). Natural selection. IV. The Price equation. Journal of Evolutionary Biology, 25, 1002–1019.

Derive other fundamental equations



[1] Queller, D. C. (2017). Fundamental theorems of evolution. The American Naturalist, 189:345-353.

My goal: starting point is unclear

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- Start with the Price equation and add ecology?
- Start somewhere else and derive Price?
- Is this even possible?
- If it's possible, it will look obvious in hindsight

The UNICOP team

Leipzig in September 2022

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- Confusion about the question
- Separated project aims
- An attempt at an answer:

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$$iN + \Delta\bar{z} = i\left(1 + \bar{w} - \bar{\delta}\right)N + \frac{1}{\bar{w}}Cov\left(z, w\right) + \frac{1}{\bar{w}}E\left(w\Delta z\right).$$

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  - "It's not *wrong*" - Séb
  - "Brad, that's cheating" -Théo

Montpellier in June 2023: Not much progress

On the backburner until January 2024

On the backburner until January 2024

Working day and night back and forth

Finally a way forward, and fundamental ecology

- Evolution: Price Equation
- Ecology: Exponential growth

$$N_{t+1} = N_t + Births - Deaths$$

[1]Gotelli, NJ (2001). A Primer of Ecology. Sinauer Associate. Inc. Sunderland, MA.

[2]Rockwood, LL (2006). Introduction to population ecology. Blacwell. Malden, MA

[3]Turchin, P (2001). Does population ecology have general laws? Oikos, 94(1), 17-26 [PDF]

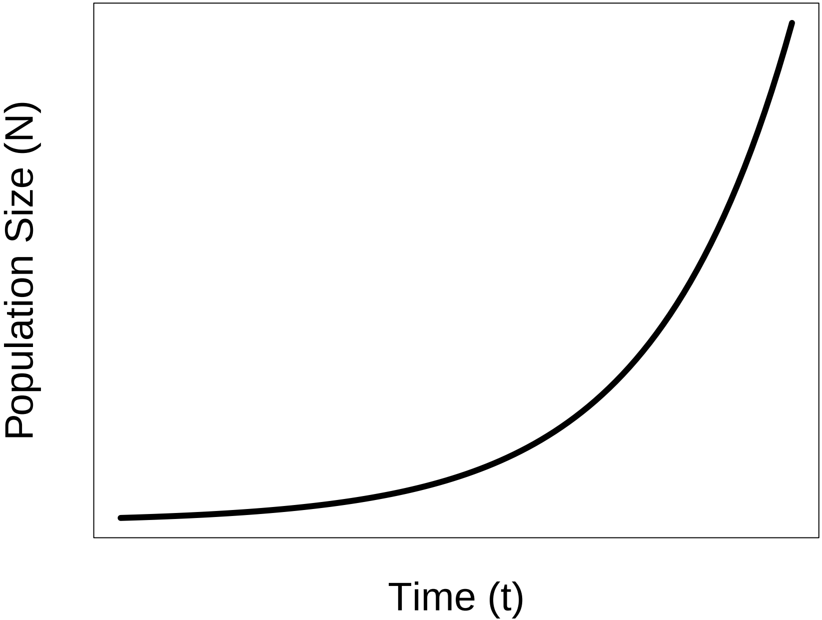
Finite rate of increase for a population

$$N_{t+1} = N_t(1 + b - d)$$

$$\lambda = (1 + b - d)$$

$$N_{t+1} = N_t \lambda$$

Finite rate of increase for a population



Finally a way forward, and fundamental ecology

Evolution: Price Equation

$$\bar{w}\Delta\bar{z} = Cov\,(w, z) + E\,(w\Delta z)$$

Ecology: Exponential growth

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Nearly there: the unicorn equation

As expected, the answer is obvious in hindsight.

A fundamental equation for ecology and evolution

$$\Omega = \sum_{i=1}^{N} \left(\beta_i - \delta_i + 1\right)\left(z_i + \Delta z_i\right)$$

A fundamental equation for ecology and evolution

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- Ω: Some summed quantity
- N: Population size
- i: Individuals in population
- β: Births attributable to i
- δ: Death indicator variable
- z_i: Character of i

Ecology: Character species identity ($z = 1$), ($\Delta z = 0$)

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$$N_{t+1} = N_t + Births - Deaths$$

$$N_{t+1} = N_t (1 + \beta - \delta) = N_t \lambda$$

Evolution: Character individual trait (z_i)

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$$\Omega = \sum_{i=1}^{N} (\beta_i - \delta_i + 1)(z_i + \Delta z_i)$$

Define fitness, $w_i = \beta_i - \delta_i + 1$. Substitute,

$$\Omega = \sum_{i=1}^{N} (w_i z_i + w_i \Delta z_i)$$

$$\frac{1}{N}\Omega = \frac{1}{N}\sum_{i=1}^{N} (w_i z_i) + \frac{1}{N}\sum_{i=1}^{N} (w_i \Delta z_i)$$

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Rewrite as expected values,

$$\frac{1}{N}\Omega = E\left(wz\right) + E\left(w\Delta z\right).$$

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[1] Frank, Steven A (2015) "D'Alembert's direct and inertial forces acting on populations: The Price equation and the fundamental theorem of natural selection." Entropy 17: 7087–7100.

[2] Frank, Steven A (2016) "Common probability patterns arise from simple invariances." Entropy 18 (5): 1–22.

Evolution: Character individual trait (z_i)

$$\frac{1}{N}\Omega = E\left(wz\right) + E\left(w\Delta z\right).$$

Tricky step is to note $\Omega = N\bar{w}\bar{z}'$ because we need to conserve total probability[1,2], so,

$$\bar{w}\bar{z}' = E\left(wz\right) + E\left(w\Delta z\right).$$

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$$\bar{w}\bar{z}' = E\left(wz\right) + E\left(w\Delta z\right).$$

Since $COV(X, Y) = E(XY) - E(X)E(Y)$,

$$\bar{w}\bar{z}' = Cov(w, z) + \bar{w}\bar{z} + E\left(w\Delta z\right).$$

$$\bar{w}\left(\bar{z}' - \bar{z}\right) = Cov(w, z) + E\left(w\Delta z\right).$$

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$$\bar{w}\left(\bar{z}' - \bar{z}\right) = Cov(w, z) + E\left(w\Delta z\right).$$

Since $\Delta z = \bar{z}' - \bar{z}$,

$$\bar{w}\Delta\bar{z} = Cov(w, z) + E\left(w\Delta z\right).$$

We have therefore derived Price.

Who cares?

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- Derives assumed $N_{t+1} = N_t\lambda = N_t\bar{w}$
- Lifetime fitness is still β_i
- Starting point for further unification
- Ecology hiding in population genetics

The most elegant part

$$\Omega = \sum_{i=1}^{N} (\beta_i - \delta_i + 1)(z_i + \Delta z_i)$$

Fisher's fundamental theorem[1,2] $w = z$,

[1] Frank, SA (1997). "The Price equation, Fisher's fundamental theorem, kin selection, and causal analysis." Evolution 51:1712–29.

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Fisher's fundamental theorem[1,2] $w = z$,

$$\Delta \bar{w} = \frac{1}{\bar{w}} Var(w)$$

This is because $Cov(w, w) = Var(w)$.

[1] Frank, SA (1997). "The Price equation, Fisher's fundamental theorem, kin selection, and causal analysis." Evolution 51:1712–29.

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What this means is the following:

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$$\Omega = \sum_{i=1}^{N} (\beta_i - \delta_i + 1)(z_i + \Delta z_i)$$

What this means is the following:

- Rate of population growth is the first statistical moment of fitness

The most elegant part

$$\Omega = \sum_{i=1}^{N} (\beta_i - \delta_i + 1)(z_i + \Delta z_i)$$

What this means is the following:

- Rate of population growth is the first statistical moment of fitness
- Rate of adaptive evolution is the second statistical moment of fitness

Bonus for ecosystem function

$$\Omega = \sum_{i=1}^{N} \left(\beta_i - \delta_i + 1\right)\left(z_i + \Delta z_i\right)$$

We can define z as a trait (e.g., photosynthetic rate, decomposition rate, biomass) and recover Ω as a population's contribution to ecosystem function.