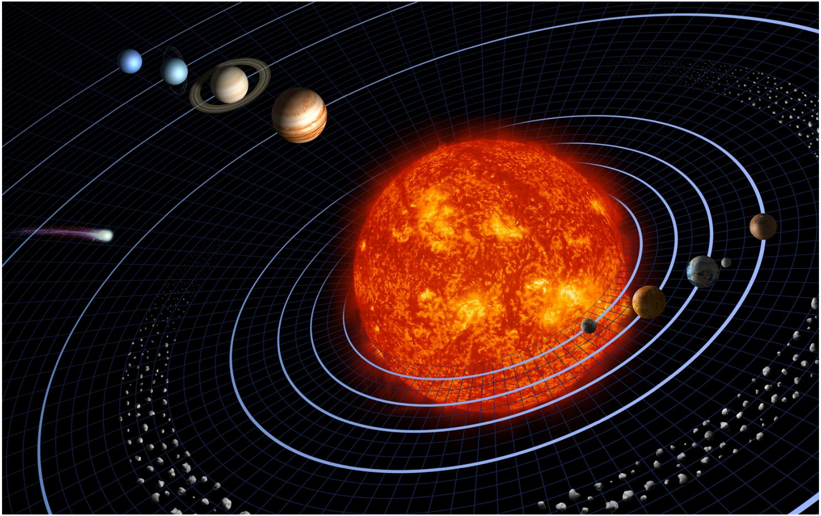
Foundations of ecological and evolutionary change

Brad Duthie and Victor Luque

Why people do science, particularly biology

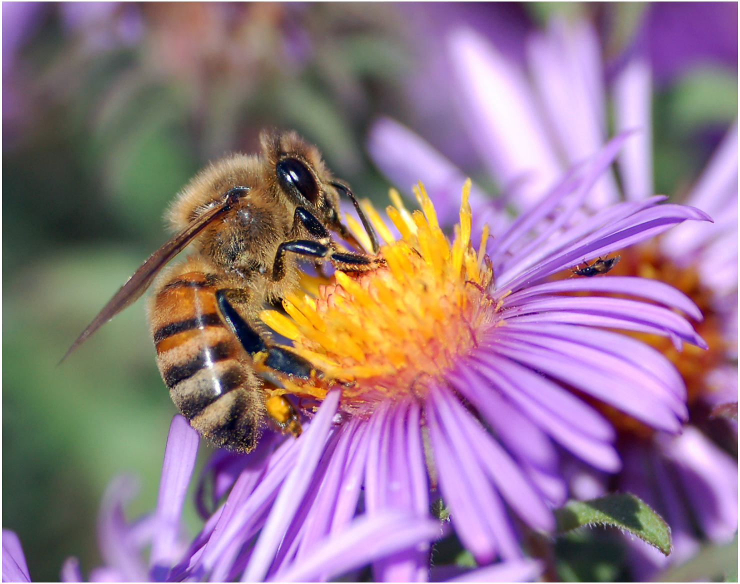
[1] Image: Gillette, B. 1972. Public Domain

Unification of celestial and terrestrial motion



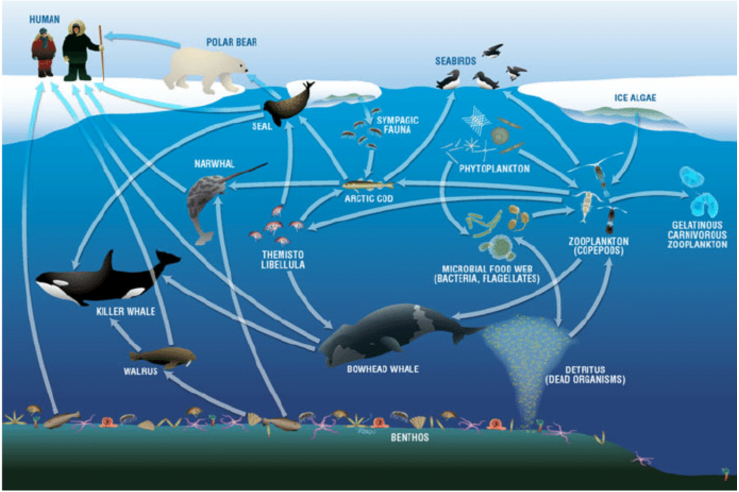
[1] Image: Smith, H and L Generosa (2006). Public Domain

Complexity of the biological sciences



[1] Image: John Severns (2006). Public Domain

Complexity of the biological sciences

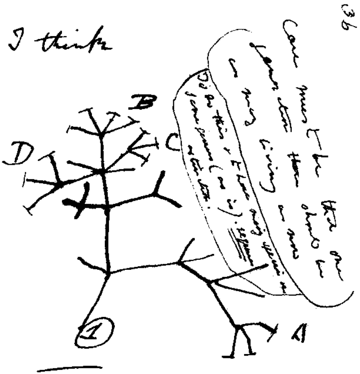


[1]Darnis, G, et al. (2012). Current state and trends in Canadian Arctic marine ecosystems: II. Heterotrophic food web, pelagic-benthic coupling, and biodiversity. Climatic Change, 115, 179-205.

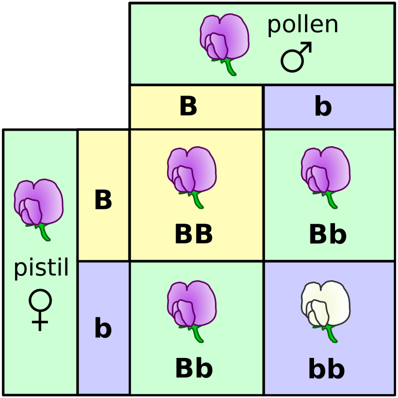
[1]Image: Darnis, G, et al. (2012). Public Domain

Unification of evolution and genetics

Darwinian evolution



Mendelian genetics



[1]Image (left): Public Domain

[2]Image (right): Madeleine Price Ball (2007). Public Domain

Unification of evolution and genetics

$$p^2 + 2pq + q^2 = 1$$

- No natural selection
- No mutation
- No migration (no gene flow)
- Infinite population size
- Mating is random
- Non-overlapping generations

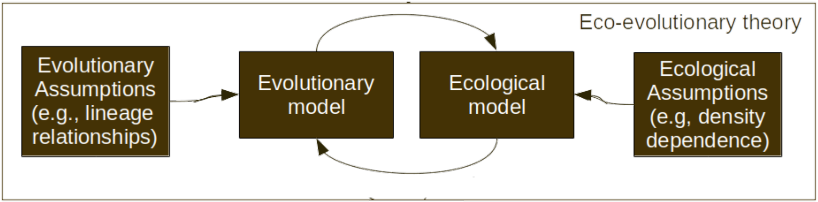
General theory of community ecology

Population genetics	**Community ecology**
Selection	Species selection
Mutation	Disperal
Gene flow	Drift
Genetic drift	Speciation

General community ecology theory focused on high-level processes[1]

[1] Vellend, M (2016). The theory of ecological communities. Monographs in population biology. Princeton University Press.

Eco-evolutionary models



Eco-evolutionary models

Lion[1] (2018)

Ecology:

$$\frac{dn_i}{dt} = r_i\left(\mathbf{E}\right) n_i$$

Evolution:

$$\frac{df_i}{dt} = f_i\left(r_i\left(\mathbf{E}\right) - \bar{r}\left(\mathbf{E}\right)\right)$$

[1] Lion, S (2018). Theoretical approaches in evolutionary ecology: environmental feedback as a unifying perspective. Am. Nat., 191:21-44

[2] Patel, S, Cortez, MH, & Schreiber, SJ (2018). Partitioning the effects of eco-evolutionary feedbacks on community stability. The Am. Nat., 191:381-394.

Eco-evolutionary models

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Evolution:

$$\frac{df_i}{dt} = f_i\left(r_i(\mathbf{E}) - \bar{r}(\mathbf{E})\right)$$

Patel et al.[2] (2018)

Ecology:

$$\frac{dN_i}{dt} = N_i f_i(N, x)$$

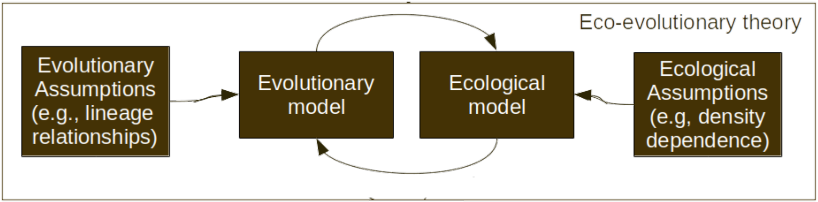
Evolution:

$$\frac{dx_j}{dt} = \epsilon g_j(N, x)$$

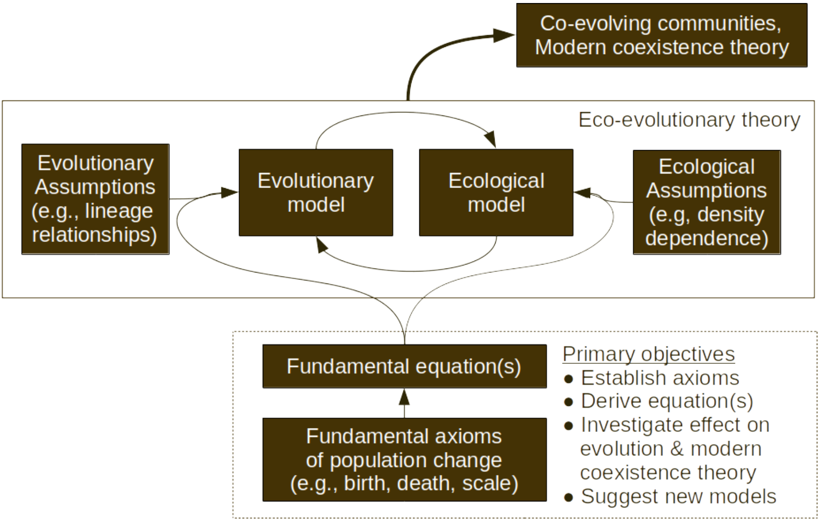
[1] Lion, S (2018). Theoretical approaches in evolutionary ecology: environmental feedback as a unifying perspective. Am. Nat., 191:21-44

[2] Patel, S, Cortez, MH, & Schreiber, SJ (2018). Partitioning the effects of eco-evolutionary feedbacks on community stability. The Am. Nat., 191:381-394.

Conceptual unification of ecology and evolution



Conceptual unification of ecology and evolution



Unification of modern coexistence theory & Price equation

Joint funding call between French Foundation for Research on Biodiversity and German Centre for Integrative Biodiversity Research (iDiv): CESAB-sDIV SYNERGY

The UNICOP team in Montpellier (summer 2023)

A different role of theory (not doing modelling)

- Not making assumptions or predictions

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- Defining population change in an eco-evo context

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$$y = \beta_0 + \beta_1 x$$

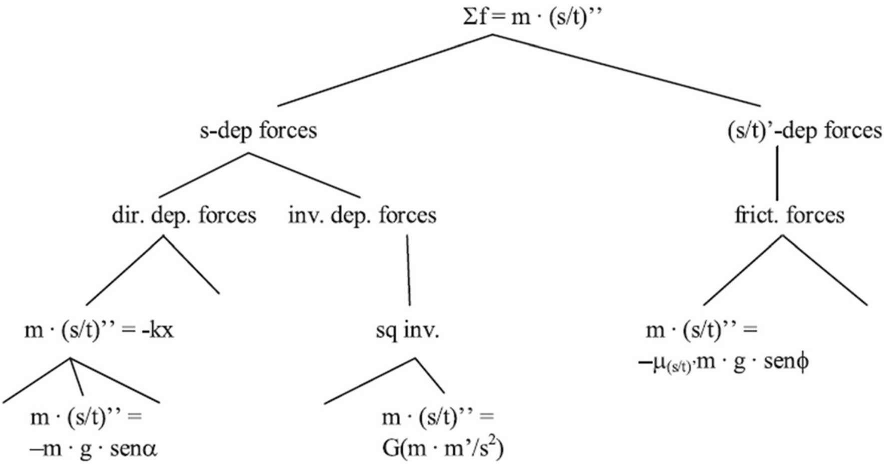
A different role of theory (not doing modelling)

- Not making assumptions or predictions
- Defining population change in an eco-evo context
- Framework for models (meta-modelling)
- A rough analogy,

$$y = \beta_0 + \beta_1 x$$

- 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:

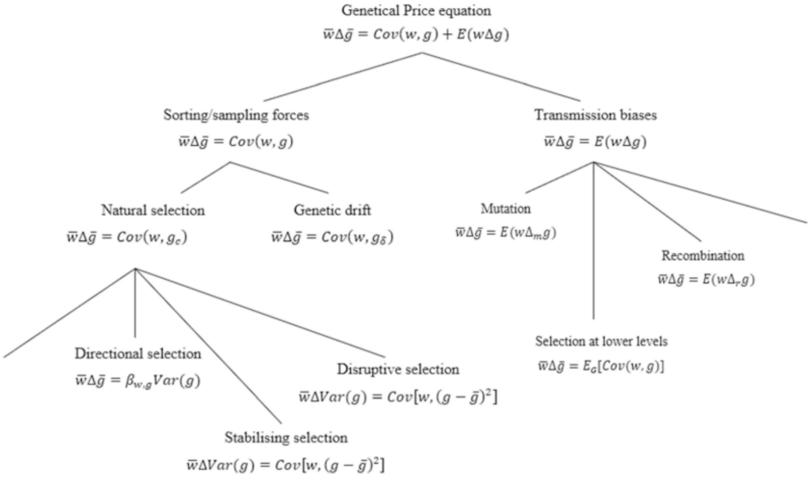
$$\Delta\bar{z} = \sum q_i \left(\frac{w_i}{\bar{w}} - 1\right) z_i + \sum q_i \frac{w_i}{\bar{w}} (\Delta z_i)$$

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

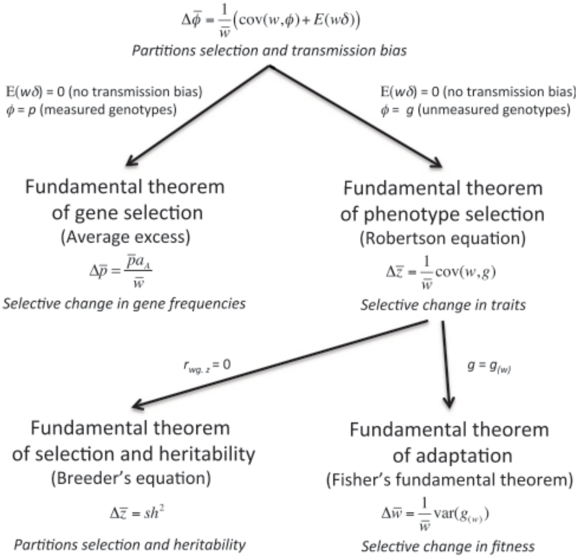
$$\bar{w}\Delta\bar{z} = Cov\left(w, z\right) + E\left(w\Delta z\right)$$

[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, DC (2017). Fundamental theorems of evolution. The American Naturalist, 189:345-353.

Evolution of non-biological systems

- Archaeological artefacts[1]
- Musical properties[2]

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[1] Brantingham, PJ (2007). A unified evolutionary model of archaeological style and function based on the Price equation. American Antiquity 72:395–416.

[2] MacCallum, RM, et al. (2012). Evolution of music by public choice. PNAS 109:12081–12086.

[3] Frank, SA (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.

[3] Frank, SA (2012). Natural selection. V. How to read the fundamental equations of evolutionary change in terms of information theory. Journal of Evolutionary Biology, 25:2377-2396.

Generality of the Price equation

Evolution of non-biological systems

- Archaeological artefacts[1]
- Musical properties[2]

Synthesis across disciplines

- D'Alembert's principle of mechanics[3]
- Information theory[4]

[1]Brantingham, PJ (2007). A unified evolutionary model of archaeological style and function based on the Price equation. American Antiquity 72:395–416.

[2]MacCallum, RM, et al. (2012). Evolution of music by public choice. PNAS 109:12081–12086.

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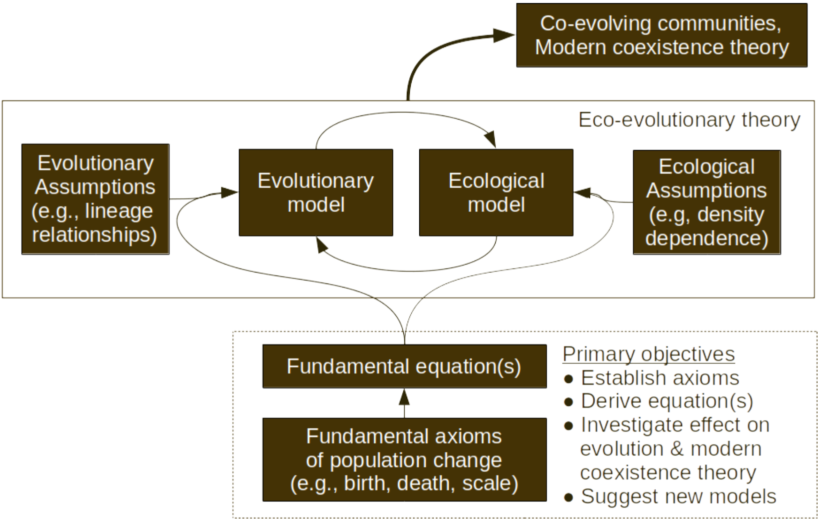
Conceptual unification of ecology and Price equation



Links between ecology and the Price equation

Ecosystem function loss due to species loss[1]

$$\Delta T = \bar{z}\Delta s + Sp(w, z) + \sum_i w_i \Delta z_i$$

[1] Fox, JW (2006). Using the price equation to partition the effects of biodiversity loss on ecosystem function. Ecology, 87(11), 2687-2696.

[2] Collins, S & Gardner, A (2009). Integrating physiological, ecological and evolutionary change: A Price equation approach. Ecology Letters, 12(8), 744-757.

Links between ecology and the Price equation

Ecosystem function loss due to species loss[1]

$$\Delta T = \bar{z}\Delta s + Sp(w, z) + \sum_i w_i \Delta z_i$$

Community trait change: Physiology, evolution, ecology[2]

$$\Delta \bar{z} = E_I\left(E_{Ji}\left(\Delta z_{ij}\right)\right) + E_I\left(cov_{Ji}\left(w_{ij}, z'_{ij}\right)\right) + cov_I\left(w_i, z'_i\right)$$

[1] Fox, JW (2006). Using the price equation to partition the effects of biodiversity loss on ecosystem function. Ecology, 87(11), 2687-2696.

[2] Collins, S & Gardner, A (2009). Integrating physiological, ecological and evolutionary change: A Price equation approach. Ecology Letters, 12(8), 744-757.

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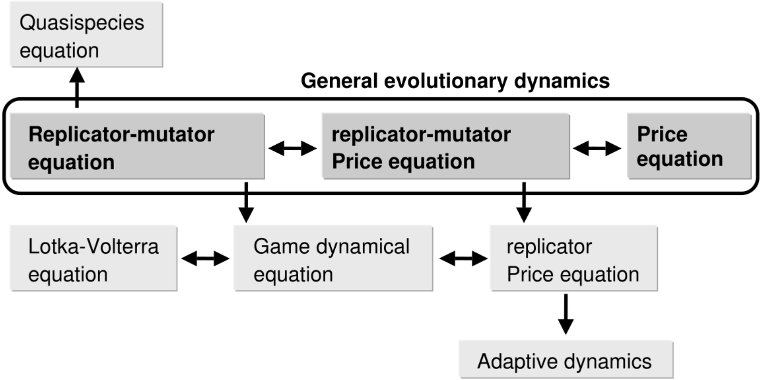

- Figure 1 from Page & Nowak[1]
- Relies on *relative* species frequenies

[1] Page, KM & Nowak, MA (2002). Unifying evolutionary dynamics. Journal of Theoretical Biology, 219(1), 93–98.

Reconciling evolutionary change and population growth

- Start with Price equation and add ecology?
- Start elsewhere and derive the Price equation?

[1] Image: Eneas De Troya (2006).

The fundamental equation of ecology

- Evolution: Price Equation
- Ecology: Births and deaths

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

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[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]

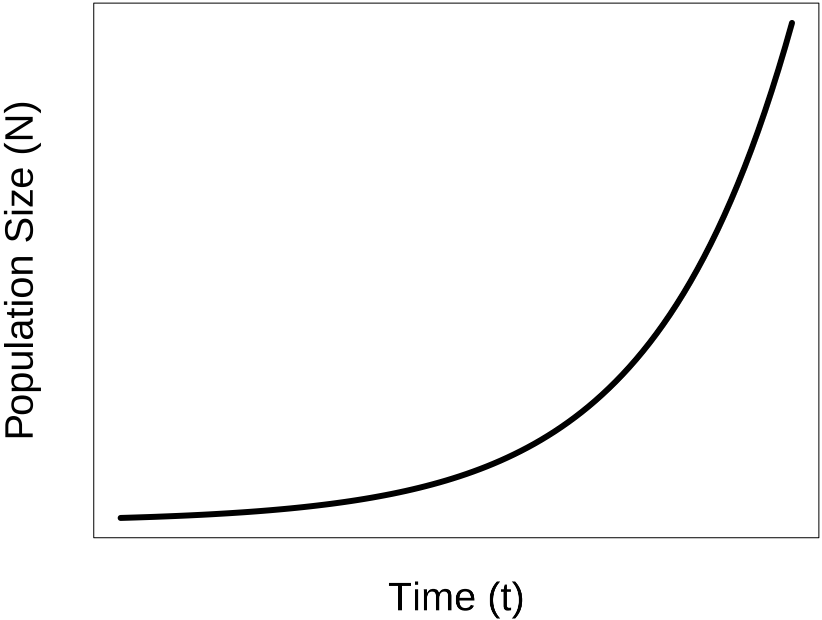
Finite rate of increase for a population

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

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

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

Finite rate of increase for a population



Evolution: Price Equation

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

Ecology: Exponential growth

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

The unifying equation

- No systematic approach
- Individual birth, death, characteristics
- Deductive exploration

The unifying equation

- No systematic approach
- Individual birth, death, characteristics
- Deductive exploration

As expected, the answer is obvious in hindsight.

A fundamental equation for ecology and evolution

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

A fundamental equation for ecology and evolution

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

- 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 ($z = 1$), ($\Delta z = 0$)

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

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

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

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

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

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

Evolution: Character individual trait (z_i)

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

Evolution: Character individual trait (z_i)

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

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

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

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

Evolution: Character individual trait (z_i)

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

Evolution: Character individual trait (z_i)

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

Rewrite as expected values,

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

Evolution: Character individual trait (z_i)

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

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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,

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

[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.

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Evolution: Character individual trait (z_i)

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

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

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

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

Evolution: Character individual trait (z_i)

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Evolution: Character individual trait (z_i)

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

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.

A formal definition of eco-evolutionary change

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

Formalises ecology & evolution

A formal definition of eco-evolutionary change

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Formalises ecology & evolution

- No simplifying assumptions

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Formalises ecology & evolution

- No simplifying assumptions
- Complete and exact (closed populations)

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Formalises ecology & evolution

- No simplifying assumptions
- Complete and exact (closed populations)
- Ecology: $\beta_i - \delta_i + 1$

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Formalises ecology & evolution

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A formal definition of eco-evolutionary change

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

Formalises ecology & evolution

- No simplifying assumptions
- Complete and exact (closed populations)
- Ecology: $\beta_i - \delta_i + 1$
- Evolution: $z_i + \Delta z_i$
- Ecology required for selection or drift

Confirmations from a formal definition

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

Formalises fitness and population growth:

Confirmations from a formal definition

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

Formalises fitness and population growth:

- **Fitness:** $\bar{w} = \lambda = \beta - \delta + 1$

Confirmations from a formal definition

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Formalises fitness and population growth:

- **Fitness:** $\bar{w} = \lambda = \beta - \delta + 1$
- Derives assumed $N_{t+1} = N_t \lambda = N_t \bar{w}$

Confirmations from a formal definition

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Formalises fitness and population growth:

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- Derives assumed $N_{t+1} = N_t \lambda = N_t \bar{w}$
- Lifetime fitness is still β_i

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

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- Starting point for further unification

Confirmations from a formal definition

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Formalises fitness and population growth:

- **Fitness:** $\bar{w} = \lambda = \beta - \delta + 1$
- Derives assumed $N_{t+1} = N_t \lambda = N_t \bar{w}$
- Lifetime fitness is still β_i
- Starting point for further unification
- Build upon for community ecology

An elegance in two fits

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

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.

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

An elegance in two fits

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

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.

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

An elegance in two fits

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

What this means is the following:

An elegance in two fits

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

What this means is the following:

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

An elegance in two fits

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

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

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

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.

Foundations of ecological and evolutionary change

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

arXiv > q-bio > arXiv:2409.10766

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Quantitative Biology > Populations and Evolution

[Submitted on 16 Sep 2024]

Foundations of ecological and evolutionary change

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Biological evolution is realised through the same mechanisms of birth and death that underlie change in population density. The deep interdependence between ecology and evolution is well-established, but much theory in each discipline has been developed in isolation. While recent work has accomplished eco-evolutionary synthesis, a gap remains between the logical foundations of ecology and evolution. We bridge this gap with a new equation that defines a summed value for a characteristic across individuals in a population, from which the fundamental equations of population ecology and evolutionary biology (the Price equation) are derived. We thereby unify the fundamental equations of population ecology and biological evolution under a general framework. Our unification further demonstrates the equivalence between mean population growth rate and evolutionary fitness, shows how ecological and evolutionary change are reflected in the first and second statistical moments of fitness, respectively, and links this change to ecosystem function.

[1] Duthie, AB, & Luque, VJ (2024). Foundations of ecological and evolutionary change. arXiv preprint arXiv:2409.10766.