

A unifying equation of ecology and evolution

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Background

Theoretical unification of phenomena once assumed to be disparate is a powerful tool for scientific advancement. Such unification has therefore been a major goal in scientific research throughout history (Kitcher 1993), and its value is perhaps most evident in reconciling unconnected models and revealing new and unexpected empirical predictions. In theoretical physics, Newton’s unification of celestial and terrestrial motion, and Maxwell’s unification of electricity and magnetism, are among the most important advances in scientific history. Likewise, in the life sciences, the modern synthesis of natural selection and Mendelian inheritance revolutionised how mechanisms underlying evolution are understood and applied.

Three major evolutionary mechanisms (natural selection, genetic drift, and gene flow) are instantiated through a combination of different ecological factors (Connor and Hartl 2004). Most notably, change in both the traits and size of a closed population are caused by individual birth and death.

Nevertheless, until relatively recently, evolutionary biology and population ecology have taken almost parallel paths for developing theory. Although many models now exist to connect evolutionary and ecological phenomena (e.g., Lion 2018; Patel, Cortez, and Schreiber 2018; Govaert et al. 2019), the foundational assumptions and equations of evolution and ecology in these models remain mostly separated conceptually. Here we propose the foundation for a different approach. Instead of joining existing fundamental models of ecology and evolution, we propose a new equation from which the most general equations of population ecology, evolution, and ecosystem function can be derived.

The fundamental equation of ecology, evolution, and ecosystem function

Our objective is to start with the most fundamental axioms underlying both ecology and evolution in all systems (Rice 2004; Rice and Papadopoulos 2009). All such systems include entities (e.g., individuals, but our framework is sufficiently general such that entities can be anything discrete). Entities are introduced into the population through birth and removed from it through death. Entities are defined by some property, which might be a species identity (ecology) or a trait (evolution).

Let β_i be the number of births attributable to entity i . Let δ_i indicate the death (1) or survival (0) of i . Let z_i be a property attributable to i , and Δz_i be any change in z_i from one time step t to the next $t + 1$. Let the number of entities in the population be N . Finally, let Ω be a summed property across N entities,

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

From the above equation, we can derive the most fundamental equations of population ecology and evolutionary biology through an appropriate interpretation of z_i .

Population ecology

Assume that z_i defines the identity of i belonging to the population. In other words, we set $z_i = 1$ to simply indicate that i is a member of the population. Further, we make the standard population ecology assumption that entities (now specifically individual organisms) are identical and do not change species. To define this formally, we set $\Delta z_i = 0$ and note that we can drop the subscript i such that $\beta_i = \beta$ and $\delta_i = \delta$. In this case, we have,

$$\Omega = \sum_{i=1}^N (\beta - \delta + 1).$$

Summing up from 1 to N , we can rewrite the above,

$$\Omega = N (\beta - \delta + 1).$$

We can now interpret Ω as the population size in $t + 1$, N_{t+1} , and note that $N\beta$, $N\delta$, and N are the total births, total deaths, and size of the population at t , respectively,

$$N_{t+1} = \text{births} - \text{deaths} + N_t.$$

Alternatively, if we define $\lambda = 1 + \beta - \delta$, then we can rewrite,

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

This equation is fundamental in the sense that the change in size of every closed population is attributable to births minus deaths. We can build upon this by structuring the population (e.g., into age or stage classes), or by including space or density-dependent effects, but all of these different mechanisms of population change are ultimately realised through the birth and death of individuals. Consequently, the above equation describes the change in every closed population from one time step to the next.

It is worth pointing out now that λ is going to come out as equivalent to mean fitness \bar{w} in working out the link to the Price equation below. We could therefore write the above as, $N_{t+1} = N_t \bar{w}$ with $w = \bar{w}$ then being the fitness of all individuals in the population. Next, we will derive the Price equation from the fundamental equation.

Evolutionary change

Deriving Price takes a few more steps. We can start by rearranging the original equation,

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

As noted in the previous section, we can define fitness,

$$w_i = \beta_i - \delta_i + 1$$

The fitness of an individual from one time step to the next equals the number of offspring of the individual (β_i), minus 1 if the individual has died ($\delta_i = 1$) or 0 if the individual has not died, plus 1. Note that in addition to offspring number, the longevity of the individual matters in terms of fitness. If the individual

dies, then fitness is simply β_i . If the individual lives, then fitness is $\beta_i + 1$. This is conceptually satisfying because an individual that lives from t to $t + 1$ should have higher fitness than an individual that dies, even if both have the same reproductive output. With this definition of fitness, we substitute,

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

We can break this down further,

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

We can multiply each side by $1/N$,

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

On the right-hand side of the equation above, this gives us the expected values within the summation,

$$\frac{1}{N}\Omega = E(w_i z_i) + E(w_i \Delta z_i).$$

The left-hand side requires a bit more explanation. What we have above is the total sum trait values z across the entire population at $t + 1$ divided by the number of individuals (N) in the population at t . What we need is the mean z across N in our *original* population. In other words, dividing Ω by N will include contributions to the sum trait value from the *new* population at $t + 1$ on the left-hand side of the equation. We therefore cannot treat Ω/N as the mean of z' because we need to weigh N by the mean fitness of the population at t to account for any change in population size from t to $t + 1$. For example, if mean fitness is 2 (i.e., $\bar{w} = 2$), then half as many individuals from t will have contributed to Ω in $t + 1$ (i.e., there are N individuals at t and $2N$ individuals at $t + 1$). We therefore need to multiply the mean trait value of \bar{z}' (at $t + 1$) by the mean fitness of \bar{w} at t to recover the mean contribution of the N individuals at t to the total Ω . Consequently, $\Omega = N\bar{w}\bar{z}'$. That is, the number of individuals at t , times the mean fitness at t , times the mean of z at $t + 1$ (\bar{z}'). We can therefore rewrite,

$$\bar{w}\bar{z}' = E(w_i z_i) + E(w_i \Delta z_i).$$

Rearranging this now to derive the Price equation is not difficult. First, note that we can express covariance as, $Cov(X, Y) = E(XY) - E(X)E(Y)$, and therefore $E(XY) = Cov(X, Y) + E(X)E(Y)$. Substituting into the above,

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

From here,

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

Pulling fitness out of the left-hand side,

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

Since we define $\Delta z_i = (z'_i - z_i)$,

$$\bar{w}\Delta z_i = Cov(w_i, z_i) + E(w_i\Delta z_i).$$

From the starting point of the first equation for Ω , which describes fundamental birth and death processes in a population, we can derive both the most fundamental geometric growth model of population ecology and the fundamental equation of evolution. By itself, we could also consider Ω to be a quantity of ecosystem function, in that it is the summed effect of the traits (z_i) of individual entities (i) in the population. For example, z might be interpreted as biomass or photosynthetic rate.

Discussion

To my knowledge, a fundamental equation from which geometric growth, the Price equation, and ecosystem function models can be derived has not been attempted or demonstrated. Page and Nowak (2002) showed some nice equivalences between replicator equations, Lotka-Volterra, and the Price equation, but not in quite the unifying way that I think we show here.

I believe that there is conceptual and philosophical merit in this work. The equation certainly was not obvious at the outset of this effort, although if correct and useful, it will almost certainly appear obvious in hindsight. In working through this result, there are some issues that I think become clearer with this unifying approach. For example, the equivalence between mean fitness (\bar{w}) and population growth rate (λ) is confirmed from first principles (Lion 2018).

Assumptions of ecological and evolutionary models are also made clearer, I think. And with this formalism, we can more clearly identify the kinds of processes that are enacted through ecology, evolution, or both. For example, demographic stochasticity, which is defined by fluctuations caused by the probabilistic nature of birth and death, will clearly affect Ω and therefore have joint effects on population ecology and evolution. Any model that includes demographic stochasticity should therefore do so in a way that has consistent and simultaneous effects on both population and evolutionary dynamics. In contrast, some processes are relevant to only ecology or evolution.

In population ecology, the assumption that individuals within a species are identical and do not change is formalised by setting $z_i = 1$, $\Delta z_i = 0$, $\beta_i = \beta$, and $\delta_i = \delta$. Expansions from the equation for geometric growth could be made to model population structure. The Price equation is established as the fundamental equation of evolution, and our work here shows how evolutionary change is grounded in the birth and death of discrete entities.

There are other avenues of potential interest. For example, it is potentially interesting that the derivation of geometric growth takes considerably fewer steps than the Price equation. It also seems relevant that neither the ecology nor evolution seem to take precedence, in the sense that one is more fundamental and derived from the other. It also might be interesting to think more about the conservation of total probability (Frank 2020) and where it first becomes relevant above.

References

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