Foundations of community ecology: Supporting Information 1

A. Bradley Duthie[1,a,*] and Victor J. Luque[2,a]

[1] Department of Biological and Environmental Sciences, University of Stirling, Stirling, Scotland [2] Department of Philosophy, University of Valencia, Valencia, Spain [*] Corresponding author: alexander.duthie@stir.ac.uk [a] Equal contribution

This supporting information demonstrates how to derive well-established models in population ecology and evolutionary biology from equation 1 in the main text,

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

In the main text, we derived both the Price equation and the birth-death model from the above. Here we integrate interactions between individuals to recover density-dependent population growth, and we integrate groups within the population to recover multi-level selection. Finally, we integrate both to model a system in which multi-level selection and density dependent population change occur simultaneously. We can do this in a way that clarifies model assumptions by allowing an individual j to modulate the birth or death of the focal individual i.

Density-dependent population growth

There are two potential ways to model the incorporation of density dependence into population growth. We start with what is likely the most familiar model focusing on individual growth rate r_i, then use a slightly different model focusing on fitness w_i. First note that here we set $\Omega = N_{t+1}$, and $z_i = 1$ and $\Delta z_i = 0$ for all individuals as in the main text. We can define $r_i = \beta_i - \delta_i$ as an individual growth rate for i (Lion 2018; Lion, Sasaki, and Boots 2023). In this case,

$$N_{t+1} = \sum_{i=1}^{N_t} \left(r_i + 1\right) \tag{S1}$$

Mathematically, the most general approach here would be to define individual growth as a function of the entire system $\mathbf{E}$, $r_i(\mathbf{E})$, where $\mathbf{E}$ is a vector with elements including any parameters potentially relevant to r_i. Taking this approach would recover a version of eqn 2 in Lion (2018) and permit any relationship between the system and a focal individual's growth. Limiting our focus to the effects of other individuals (j) and assuming that the effects of these individuals are additive, let $a_{ij|\cdot}$ be the effect of individual j on the growth rate attributable to i conditioned on all other individuals within the population such that $r_i\left(1 + \sum_{i=j}^{N} a_{ij|\cdot}\right)$ defines the realised growth rate of i,

$$N_{t+1} = \sum_{i=1}^{N_t} \left(r_i\left(1 - \sum_{i=j}^{N_t} a_{ij|\cdot}\right) + 1\right). \tag{S2}$$

Assuming that individual effects of j on i are also independent, we can remove the condition,

$$N_{t+1} = \sum_{i=1}^{N_t} \left(r_i \left(1 - \sum_{i=j}^{N_t} a_{ij} \right) + 1 \right).$$

Further assuming that all individuals have the same per capita effect such that $a = a_{ij}$ for any i and j pair (as might be reasonable given resource competition in a well-mixed population),

$$N_{t+1} = \sum_{i=1}^{N_t} \left(r_i \left(1 - aN_t \right) + 1 \right).$$

If r_i values are identical,

$$N_{t+1} = N_t + rN_t \left(1 - aN_t \right). \tag{S3}$$

Equation S3 therefore recovers a classic version of a discrete time logistic growth by making assumptions from an exact model of eco-evolutionary change.

An alternative approach would be to define model the effects of an individual j on the fitness of i (w_i), thereby replacing eqn S1 with $N_{t+1} = \sum_{i=1}^{N_t} w_i$ and replacing eqn S2 with,

$$N_{t+1} = \sum_{i=1}^{N_t} w_i \left(1 - \sum_{i=j}^{N_t} \alpha_{ij|\cdot} \right).$$

Note that we have used α_{ij} to represent the effect of j on the fitness of i for clarity in the sections below. By making the same assumptions of additivity, independence, and identical effects such that $\alpha = \alpha_{ij}$ for all j on i, and assuming fitness is equal ($w_i = \bar{w}$), we can derive,

$$N_{t+1} = \bar{w}N_t(1 - \alpha N_t). \tag{S4}$$

This is an alternative way to express logistic growth.

Multi-level selection

We can recover multi-level selection from our eqn 1. Here we derive the original form of the multi-level Price (1972) equation as it appears in eqn 3.1 of Lehtonen (2020). Individuals belong to one of K total groups where j indexes K groups and i indexes individuals. Individuals do not overlap in group membership. The size of group j is denoted as N_j. Equation S5 below uses summations to partition how individuals within each group contribute to Ω,

$$\Omega = \sum_{j=1}^{K} \sum_{i=1}^{N_j} \left(\beta_{j,i} - \delta_{j,i} + 1 \right) \left(z_{j,i} + \Delta z_{j,i} \right). \tag{S5}$$

In S5, indices $\beta_{j,i}$, $\delta_{j,i}$, and $z_{j,i}$ identify individual i in group j. For simplicity, we set $w_{j,i} = \beta_{j,i} - \delta_{j,i} + 1$ and let $\Delta z_{j,i} = 0$ (i.e., no transmission bias),

$$\Omega = \sum_{j=1}^{K} \sum_{i=1}^{N_j} w_{j,i} z_{j,i}.$$

For ease of presentation, with no loss of generality, we assume all group sizes are equal with a group size of $N_j = n$ for all j. If group sizes differ, then weighted expectations and covariances are instead needed (Lehtonen 2020). Given equal group sizes, the total number of individuals (N) equals $K \times n$, and,

$$\frac{\Omega}{Kn} = \left(\frac{1}{K}\right)\left(\frac{1}{n}\right)\sum_{j=1}^{K}\sum_{i=1}^{n} w_{j,i} z_{j,i}.$$

Rearranging,

$$\frac{\Omega}{Kn} = \frac{1}{K}\sum_{j=1}^{K}\frac{1}{n}\sum_{i=1}^{n} w_{j,i} z_{j,i}.$$

The inner summation can be rewritten as an expectation for group j,

$$\frac{\Omega}{Kn} = \frac{1}{K}\sum_{j=1}^{K} \mathrm{E}_j\left(w_{j,i} z_{j,i}\right).$$

As in the main text, we note $\mathrm{E}(XY) = \mathrm{Cov}(X, Y) + \mathrm{E}(X)\mathrm{E}(Y)$. Defining $Cov_j(w_j, z_j)$ as the covariance between $w_{j,i}$ and $z_{j,i}$ for group j,

$$\frac{\Omega}{Kn} = \frac{1}{K}\sum_{j=1}^{K} \mathrm{Cov}_j\left(w_{j,i}, z_{j,i}\right) + \mathrm{E}_j\left(w_{j,i}\right)\mathrm{E}_j\left(z_{j,i}\right).$$

We can separate the summation for each term,

$$\frac{\Omega}{Kn} = \frac{1}{K}\sum_{j=1}^{K} \mathrm{Cov}_j\left(w_{j,i}, z_{j,i}\right) + \frac{1}{K}\sum_{j=1}^{K}\mathrm{E}_j\left(w_{j,i}\right)\mathrm{E}_j\left(z_{j,i}\right).$$

Using the notation $\bar{w}_j = E_j(w_{j,i})$ and $\bar{z}_j = E_j(z_{j,i})$ to indicate the expectation in group j,

$$\frac{\Omega}{Kn} = \frac{1}{K}\sum_{j=1}^{K} \mathrm{Cov}_j\left(w_{j,i}, z_{j,i}\right) + \mathrm{E}\left(\bar{w}_j \bar{z}_j\right).$$

We can also rewrite the first term on the right-hand side as an expectation,

$$\frac{\Omega}{Kn} = \mathrm{E}\left(\mathrm{Cov}_j\left(w_j, z_j\right)\right) + \mathrm{E}\left(\bar{w}_j \bar{z}_j\right).$$

We can rearrange the second term on the right-hand side ($\bar{\bar{w}}$ indicates grand mean over all groups),

$$\frac{\Omega}{Kn} = \mathrm{E}\left(\mathrm{Cov}_j\left(w_j, z_j\right)\right) + \mathrm{Cov}\left(\bar{w}_j, \bar{z}_j\right) + \bar{\bar{w}}\bar{\bar{z}}.$$

As in the main text, note that $Kn\bar{\bar{w}}$ accounts for differences in total population size from t to $t+1$, with $\bar{\bar{w}}$ being mean fitness across all groups. We can therefore set $\Omega = Kn\bar{\bar{w}}\bar{\bar{z}}'$, so,

$$\frac{Kn\bar{\bar{w}}\bar{\bar{z}}'}{Kn} - \bar{\bar{w}}\bar{\bar{z}} = \mathrm{E}\left(\mathrm{Cov}_j\left(w_j, z_j\right)\right) + \mathrm{Cov}\left(\bar{w}_j, \bar{z}_j\right).$$

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

$$\bar{\bar{w}}\Delta = \mathrm{Cov}\left(\bar{w}_j, \bar{z}_j\right) + \mathrm{E}\left(\mathrm{Cov}_j\left(w_j, z_j\right)\right). \tag{S6}$$

This recovers the multi-level Price (1972) equation (Lehtonen 2020) from a starting point of eco-evolutionary change in different groups. This starting point can be found in Lehtonen (2016) B2.I, which then derives a multi-level selection version of Hamilton's rule predicting the evolution of altruism.

Integration of ecology and evolution

For simplicity, we now focus on showing an integration between ecology and evolution using a population with no multi-level selection and let $\Delta z_{j,i} = 0$ (i.e., no transmission bias). As above in the section on density-dependent population growth, we define $w_i = \beta_i - \delta_i + 1$ and use $\alpha_{i,j}$ to represent the effect of j on the fitness of i. Our starting equation is therefore,

$$\Omega = \sum_{i=1}^{N} w_i \left(1 - \sum_{j=1}^{N} \alpha_{i,j}\right) z_i. \tag{S7}$$

We have already demonstrated that if we assume all individuals have the same effect on a focal individual such that $\alpha = \alpha_{i,j}$ for all i and j pairs, we can recover equation S4 when $z_i = 1$ and Ω is therefore interpreted as the count of entities,

$$N_{t+1} = \bar{w} N_t \left(1 - \alpha N_t\right).$$

We now start from S7 to derive $\Delta\bar{z}$. The objective is to use our definition of eco-evolutionary change to simultaneously recover how interactions between individuals affect population change and evolutionary change.

We start by dividing both sides of S7 by N,

$$\frac{\Omega}{N} = \frac{1}{N} \sum_{i=1}^{N} w_i \left(1 - \sum_{j=1}^{N} \alpha_{i,j}\right) z_i. \tag{S8}$$

We can express the right-hand side of eqn S8 as an expectation,

$$\frac{\Omega}{N} = \mathrm{E}\left(w_i \left(1 - \sum_{j=1}^{N} \alpha_{i,j}\right) z_i\right). \tag{S9}$$

We can rewrite the right-hand side in terms of covariances,

$$\frac{\Omega}{N} = \mathrm{Cov}\left(w_i \left(1 - \sum_{j=1}^{N} \alpha_{i,j}\right), z_i\right) + \mathrm{E}\left(w_i \left(1 - \sum_{j=1}^{N} \alpha_{i,j}\right)\right) \mathrm{E}\left(z_i\right). \tag{S9}$$

The expectations in the second term on the right-hand side can be replaced with overbars to represent the mean,

$$\frac{\Omega}{N} = \mathrm{Cov}\left(w_i \left(1 - \sum_{j=1}^{N} \alpha_{i,j}\right), z_i\right) + \overline{w_i \left(1 - \sum_{j=1}^{N} \alpha_{i,j}\right)} \bar{z}_i. \tag{S9}$$

In the main text, we noted that $\Omega = N\bar{w}\bar{z}'$. Here mean fitness incorporates individual interactions, therefore,

$$\Omega = N\overline{w_i\left(1-\sum_{j=1}^{N}\alpha_{i,j}\right)}\bar{z}'. \tag{S10}$$

We can therefore rewrite S9,

$$\overline{w_i\left(1-\sum_{j=1}^{N}\alpha_{i,j}\right)}\bar{z}' - \overline{w_i\left(1-\sum_{j=1}^{N}\alpha_{i,j}\right)}\bar{z}_i = \mathrm{Cov}\left(w_i\left(1-\sum_{j=1}^{N}\alpha_{i,j}\right), z_i\right). \tag{S11}$$

Noting again $\Delta\bar{z} = \bar{z}' - \bar{z}$,

$$\overline{w_i\left(1-\sum_{j=1}^{N}\alpha_{i,j}\right)}\Delta\bar{z} = \mathrm{Cov}\left(w_i\left(1-\sum_{j=1}^{N}\alpha_{i,j}\right), z_i\right). \tag{S11}$$

We can rewrite the left-hand side of S11,

$$\overline{w_i\left(1-\sum_{j=1}^{N}\alpha_{i,j}\right)}\Delta\bar{z} = \mathrm{Cov}\left(w_i - w_i\sum_{j=1}^{N}\alpha_{i,j}, z_i\right). \tag{S12}$$

The covariance term can be split without any additional assumptions,

$$\overline{w_i\left(1-\sum_{j=1}^{N}\alpha_{i,j}\right)}\Delta\bar{z} = \mathrm{Cov}\left(w_i, z_i\right) - \mathrm{Cov}\left(w_i\sum_{j=1}^{N}\alpha_{i,j}, z_i\right). \tag{S13}$$

If we are able to further assume that w_i and the summation over $\alpha_{i,j}$ are independent, then we could rewrite,

$$\overline{w_i\left(1-\sum_{j=1}^{N}\alpha_{i,j}\right)}\Delta\bar{z} = \mathrm{Cov}\left(w_i, z_i\right) - \mathrm{Cov}\left(\sum_{j=1}^{N}\alpha_{i,j}, z_i\right)\bar{w_i}. \tag{S14}$$

Partitioning fitness into different components with the Price equation is commonplace. But this derivation highlights, e.g., the ecological and evolutionary relationship between nonsocial and social components of fitness, and population size. For example, the second term on the right-hand side of S13 shows the covariance between the sum of social interactions and a trait. When traits covary with the interaction between sociality and fitness, they will have a stronger effect on trait change. The magnitude of this second term will also increase with N, which reflects the stronger effect of the interaction between sociality and fitness when there are more individuals interacting with a focal individual.

References

Lehtonen, Jussi. 2016. "Multilevel selection in kin selection language." *Trends in Ecology and Evolution* xx: 1–11. https://doi.org/10.1016/j.tree.2016.07.006.

———. 2020. "The Price Equation and the Unity of Social Evolution Theory." *Philosophical Transactions of the Royal Society B: Biological Sciences* 375: 20190362. https://doi.org/10.1098/rstb.2019.0362.

Lion, Sébastien. 2018. "Theoretical approaches in evolutionary ecology: environmental feedback as a unifying perspective." *American Naturalist* 191 (1). https://doi.org/10.1086/694865.

Lion, Sébastien, Akira Sasaki, and Mike Boots. 2023. "Extending Eco-Evolutionary Theory with Oligomorphic Dynamics." *Ecology Letters* 26 (September): S22–46. https://doi.org/10.1111/ele.14183.

Price, George R. 1972. "Extension of covariance selection mathematics." *Annals of Human Genetics* 35 (4): 485–90. https://doi.org/10.1111/j.1469-1809.1957.tb01874.x.