

Evolution and selection on multiple scales in space and time

Master thesis Mathematical Sciences

Author Martijn Bouman (5491363)
Supervisors Rutger Hermsen (Theoretical Biology)
 Martin Bootsma (Mathematical Sciences)

Utrecht University

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Abstract

In Theoretical Biology, the Price Equation is a valuable tool to describe the change in average phenotype in a population. However, the Price Equation does not describe how migration affects the average phenotype in local populations. Furthermore, on larger time scales, the mathematical meaning of the terms in the Price Equation diverges from the intuitive interpretation of most people. Also, in Theoretical Biology, concepts like 'long-term' selection versus 'short-term' selection, as well as 'local' versus 'global' selection, are sometimes discussed, yet a precise mathematical framework to describe these concepts is missing. I am proposing such a framework by introducing several extensions to the Price Equation. With use of this framework, selection, as well as other factors that can cause the average phenotype in a population to change, can be described in an exact and unambiguous way on multiple scales in space and time.

Contents

1	Introduction	4
2	Background knowledge	5
3	The meaning of the selection term	10
4	Searching for a new definition of selection	12
5	An order-dependent definition of selection	14
6	The limit definition of selection	15
7	New definitions of transmission	16
8	Migration and the local Price Equation	18
9	Multilevel selection	23
10	Extending multilevel selection with the local Price Equation	25
11	Global averages of terms in local Price Equations	29
	11.1 Making sure our terms are well-defined	29
	11.2 Calculating the other terms	30
12	Combining the local Price Equation with our limit definition of selection	32
13	Global averages of limit terms in local Price Equations	35
	13.1 Explaining the definitions	35
	13.2 Selection	36
	13.3 Transmission	37
	13.4 Migration	37
14	Conclusion and discussion	38
A	Proof of theorem 6.3	40
B	Proof of theorem 7.7 (shortened)	41
C	Proofs of theorems 8.17 and 8.18	42
D	Proof of theorem 9.10	42
E	The meaning of $\widehat{M}_a^b + \widehat{\kappa}_a^b$, \widehat{M}_a^b and $\widehat{\kappa}_a^b$	45
F	Proof of theorem 12.3 and corollary 12.4	51
G	Proof of theorem 12.9	53
H	Proof of theorem 13.6	56
I	Some derivations from section 13.4	59
	I.1 Calculation for example 9	59
	I.2 Proof of theorem 13.11	60
J	Bibliography	61

1 Introduction

The Price Equation [1] describes evolutionary change in a time interval in terms of selection and transmission. In local, non-isolated environments, evolution can also happen because of individuals migrating to and from the environment. As such, the Price Equation is not equipped to describe evolution in local, non-isolated environments. Also, as I will argue in this thesis, the correct interpretation of the terms in the Price Equation when taken over large time intervals is not obvious. This is why we need extensions to the Price Equation that will allow for a better description of evolution on multiple scales in space and time. Below I will use some examples to illustrate how this can apply to current research.

In the paper "Short-sighted evolution and the virulence of pathogenic microorganisms" [3], Levin and Bull argue that "it is possible that, for a wide variety of microparasites, [...] virulence [...] is a consequence of within-host evolution that provides no benefit to the pathogen beyond the host". They argue that a mutation that makes a pathogen more virulent will benefit that pathogen to spread through its current host, but may be a hindrance for the pathogen in the effort of infecting additional hosts. As such, such a mutation would benefit a pathogen locally (within one host) but not globally (throughout all hosts), and would help the pathogen in the short term (during the time the current host is infected) but not in the long term (in the long term, pathogens survive by spreading to different hosts). Levin and Bull formulate it like follows: "The advantage of these virulent mutant microparasites is entirely local (within the host) and short-sighted." The paper of Levin and Bull is cited many times and they are far from the only ones to have written about this idea.

Levin and Bull have an interesting idea. Unfortunately - and this is not meant as criticism - it is not a very precise idea, since it is not formulated in the language of mathematics. How even *could* it be formulated in the language of mathematics when we lack a framework to quantify what it means for a trait to be beneficial 'locally' instead of 'globally' and when it is not clear how we should compare selection on 'short' and 'long' timescales?

Another field of research where local versus global, and short-term versus long-term selection are relevant is in models from game theory that take place in some space. Let me elaborate with an example. Suppose there is a 2-dimensional space where organisms live and reproduce. Organisms can be either Cooperators or Defectors. Offspring of Cooperators will be Cooperators and offspring of Defectors will be Defectors. In addition, offspring will be born and stay in the local neighborhood of their parents. Cooperators increase the fitness of those around them, and Defectors only increase their own fitness. Hence in the short term, Defectors will do better than Cooperators i.e. leave more offspring. For this reason, in the long term Defectors will find themselves surrounded by their own offspring, who will also be Defectors. Hence in the long term, Defectors may do worse than Cooperators. Also, in any local neighborhood Defectors will outcompete Cooperators, yet a local neighborhood of Cooperators is fitter than a local neighborhood of Defectors - so even though Defectors are locally fitter than Cooperators, this does not need to be the case globally.

Models like these can be seen as simple spatial models of the 'evolution of cooperation' and have been studied by many different authors ever since Nowak and May started writing about them in 1992 [4]. Though the difference between 'short-term' and 'long-term' benefits, as well as 'local' and 'global' benefits, do play a role in models like these, they are unfortunately usually not discussed using precise mathematical definitions.

The goal of this thesis is to provide theoretical biologists with additional tools to describe evolution, in particular selection, on multiple scales in space and time. This framework will be provided by expanding on the Price Equation in multiple different ways. Since this is a math thesis, I will prove all of my important statements and theorems. As such, this thesis is focused on mathematical rigour more so than on practical examples. Researchers should be able to use the toolbox provided in this thesis to make precise statements about their own practical examples, though.

In section 2 I introduce the Price Equation and give background knowledge on the subject. I am also introducing many of the mathematical definitions that will be used throughout the rest of the thesis. In section 2 I am essentially summarizing literature in Theoretical Biology, except that I use more mathematical rigour than one would usually find within this literature. As such, none of the concepts discussed in this chapter are new, but some of their mathematical formulations are.

In section 3 I introduce a potential problem with the interpretation of the Price Equation that especially comes up when one tries to apply the Price Equation to large time scales. Up to section 7 I will discuss this problem, introducing new definitions to solve this problem, and discussing my new definitions. These sections

are about my own work only and do not feature a review of literature.

The sections in this thesis can be read in various orders. Sections 8 up to section 11 can be read before sections 3 up to 7. In section 8 I introduce the local Price Equation, which is an extension to the Price Equation introduced in section 2 that can describe effects of migration on average population phenotype. The local Price Equation was contrived by my supervisor, Rutger Hermsen, and refined by me. In section 9 we return to the literature; here I introduce the concept of multilevel selection as invented by Price. In section 10 I show that the Price approach to multilevel selection, as discussed in section 9, can also be described, and even extended, by using concepts from section 8. Selection is only one term in the local Price Equation and in section 11 I show how the other terms in the local Price Equation can also be described on multiple (spatial) levels. Sections 10 and 11 fully feature my own work, and do not discuss literature.

Sections 12 and 13 combine the work from sections 3 to 7 and from sections 8 to 11. These sections do not feature any literature.

In section 14 I give a brief review of the progression made in the previous sections and will return to examples from current research to discuss the applicability of my work.

Many technical details from different sections are presented in the appendix.

2 Background knowledge

In biology, the word ‘fitness’ has an intuitive meaning to most people. The fitness of an organism describes how well adapted it is to its environment and how much offspring it will produce. Similarly, most people have an intuition on what ‘(natural) selection’ means. This intuition will often be like follows: If a trait is selected for, then that means that organisms with that trait will tend to have a higher fitness than organisms without that trait. In the last century, theoretical biologists have produced a mathematical formalism that is aimed to describe people’s intuition on concepts like these in a rigorous and quantifiable way, in particular Price [1] [2]. In this section, we will introduce some of these mathematical formulations. For simplicity, we will focus on replicators that reproduce asexually, though all of our definitions can be easily extended to include sexual reproduction. To start with, we will describe the concept of ‘fitness’ in a precise way in definitions 2.1 and 2.3. Definition 2.1 is the more wordy of the two, while definition 2.3 is more math focused.

Definitions 2.1. Consider a time interval $I \subseteq \mathbb{R}$ and a set of *replicators*. Each replicator lives in a uniquely defined time interval in the form $[a, b) \cap I$, $a < b$, $a, b \in \mathbb{R}$, and is *alive* at a time $t \in I$ if and only if $t \in [a, b)$. When a replicator lives in a time interval $[a, b) \cap I$ we say that the replicator is *born* at time a if $a > \inf_{t \in I}(t)$ and has *died* at time b if $b \in I$. Whenever a replicator is born at time a , it is necessarily the *child* of another unique replicator alive within a time interval $[c, d)$ with $c < a \leq d$. This other replicator is said to have *reproduced* at time a . (Note that although we do not allow a replicator to reproduce after its moment of death, we do allow it to reproduce at the exact moment of its death. The reason behind this choice will be discussed in remark 7.1.) The *line of descendants* of a replicator i is the set of all replicators that are a child of i , or a child of a child of i , etc., or i itself. The line of descendants *after a time t* of replicator i is the line of descendants of i excluding the descendants of children of i that are born before or at time t . Let i be some replicator that lives in some time interval $[c, d)$, and let $c \leq a < d$. The *realised fitness of i over the time interval $(a, b]$* , called $W_a^b(i)$, is the number of replicators for which the following statements both hold:

1. They are in the line of descendants after time $t = a$ of replicator i ;
2. They are alive at time b .

For now, we will illustrate our definition of realised fitness with in example 1 and will address some seeming oddities in our definitions in remark 2.2.

Example 1. See figure 1 for an illustration of the following description of events. Suppose that a replicator (red) gets a child (blue) at time $t_1 < a$ and another child (green) at time $t_2 > a$. That child gets another child (purple) at time $t_3 > t_2$ with $t_3 < b$. Then the realised fitness W_a^b of this (red) replicator is equal to 3, since the replicators in its line of descendants after time a that are alive at time b consists of 3 replicators: red, green and purple (blue was born before time a so does not count). The red replicator dies at a time $t_4 < c$. This means its realised fitness W_a^c is equal to 2; this is 1 lower than W_a^b since the red replicator no longer counts towards its own fitness.

Remark 2.2. It may seem arbitrary that we defined replicators to live in halfopen intervals in the form $(c, d]$ instead of e.g. in closed intervals in the form $[c, d]$. This is not the case. Let i be a replicator and let a a moment

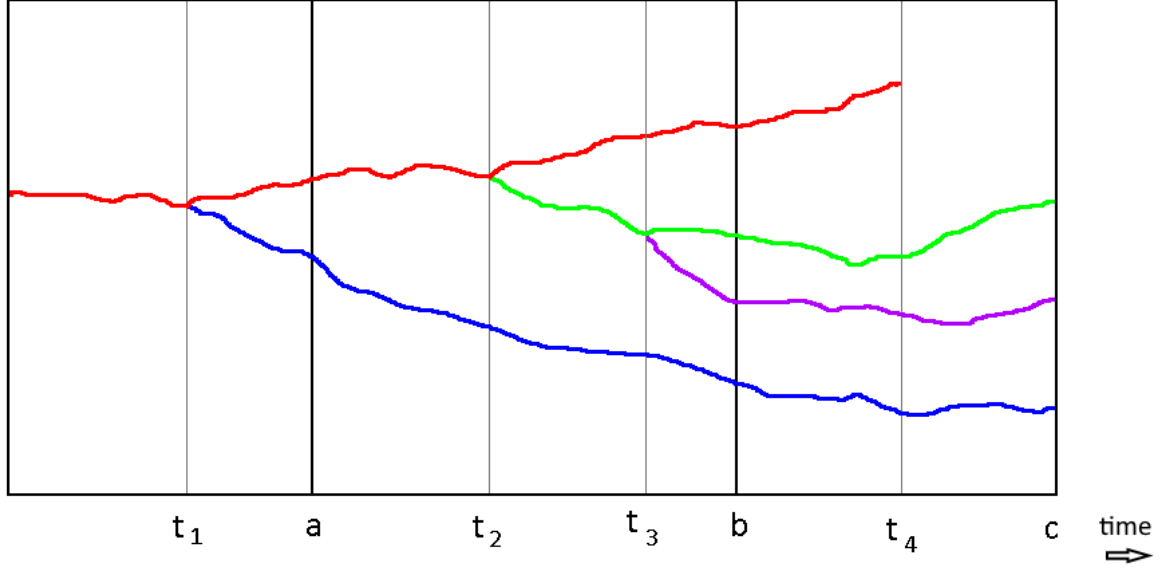


Figure 1: The horizontal axis represents time. The vertical axis does not matter, but can represent space. The red replicator gives birth to the blue replicator at time t_1 and to the green replicator at time t_2 , who in turn gives birth to the purple replicator at time t_3 . The fitness of the red replicator over the time interval $(a, b]$ is equal to 3 since at time b , that is the size of its line of descendants after time a . Since the blue replicator was born before time a , it does not count. The purple replicator does count, though. Since the red replicator dies at time t_4 , its fitness over the time interval $(a, c]$ equals 2.

before its death, but not before its birth. If i reproduces or dies at some moment in time b , then we want this to be reflected in the term $W_a^b(i)$. This can only be the case if replicators live in halfopen time intervals in the form $(c, d]$.

It also may seem odd that we have defined fitness over halfopen time intervals of the form $(a, b]$ while our replicators live in halfopen intervals of the *different* form $[c, d)$. The reason is as follows. Suppose some replicator i lives in some time interval $[c, d)$, with $a \in [c, d)$, and you want to know $W_a^b(i)$. Suppose you can search for all the details about the birth and death events of all the replicators, i.e. the times of the birth and death events, and who gave birth to who and who died. In what time interval lie the birth and death events that you need to know in order to calculate $W_a^b(i)$? The answer is the time interval $(a, b]$. Births and deaths at time a are not relevant to you, but births and deaths at time b are.

Often in nature we cannot distinguish between children and parents after a replication event. After a bacteria reproduces by splitting into two, it is arbitrary which of the two new bacteria you would label to be the ‘child’. Luckily, our definition of realized fitness is invariant under which bacteria we label to be the child. After hearing this, many mathematicians would point out that if realized fitness is invariant under labeling, then there must exist an alternative definition of realized fitness that does not *use* labeling. This is indeed correct. Below I will give that definition.

Definitions 2.3. Let there be a time interval $I \subseteq \mathbb{R}$. For every $t \in I$, we define a set of replicators R_t . For all $a, b \in I$, $a \leq b$, let $\text{anc}_{a,b} : R_b \rightarrow R_a$ be a well-defined function that describes which replicator in R_a is called the ‘ancestor’ of some replicator in R_b . As such, if $i \in R_c$ and $b \leq c$ then $\text{anc}_{a,c}(i) = \text{anc}_{a,b}(\text{anc}_{b,c}(i))$ (i.e. the ancestor of your ancestor is your ancestor). The realized fitness over the time interval $(a, b]$, called $W_a^b : R_a \rightarrow \mathbb{N}$, is defined as the following.

$$W_a^b(i) = |j \in R_b : \text{anc}_{a,b}(j) = i|. \quad (2.1)$$

To avoid clutter, for any $s \geq t$, $s, t \in I$, we will write $\text{anc}_t \equiv \text{anc}_{t,s}$ whenever it is clear what we mean. In the above equation for example, we could as well write

$$W_a^b(i) = |j \in R_b : \text{anc}_a(j) = i|, \quad (2.2)$$

since the fact that $j \in R_b$ makes it clear that anc_a is a function from R_b to R_a .

The above definition coincides with our old one if the function $\text{anc}_{a,b}(i)$ outputs the replicator living at time a for which $i \in R_b$ is in its line of descendants after time a .

From now on, we will refer to realised fitness simply as *fitness*.

Remark 2.4. In reality, fitness is the expected value of realised fitness. Since we only consider realised fitness, we will refer to ‘realised fitness’ as ‘fitness’ without running into problems.

Remark 2.5. Fitness for a system with sexual reproduction uses the same formalism, except that children only add $\frac{1}{2}$ to one’s fitness, grandchildren only $\frac{1}{4}$, and so on. (These numbers can be higher when sexual reproduction with related individuals is involved. For example, if two of your children get a child together, this grandchild of yours is counted ‘double’ and so counts as $\frac{1}{2}$ towards your fitness instead of $\frac{1}{4}$). In this thesis, we will not consider sexual reproduction.

Definitions 2.6. From now on, I will always be an interval in \mathbb{R} , even when we do not explicitly mention it.

For all $t \in I$ we define

$$N_t \equiv |R_t| \tag{2.3}$$

as the population size at time t . Let f be any property of replicators. Throughout this thesis, we will use the following notation to denote the average of f at time t :

$$\mathbf{E}_t(f) \equiv \bar{f}_t \equiv \frac{1}{N_t} \sum_{i \in R_t} f(i). \tag{2.4}$$

Let g be another property of replicators. We define the covariance between f and g using the previous notation in the following way.

$$\text{Cov}_t(f, g) \equiv \mathbf{E}_t(fg) - \mathbf{E}_t(f)\mathbf{E}_t(g). \tag{2.5}$$

Note that $\mathbf{E}_t(f)$ can be interpreted as the expected value of the experiment in which one measures the value f of a random replicator at time t , where every replicator has an equal probability of being measured. It is easier, though, to think of $\mathbf{E}_t(f)$ as a statistical average, rather than an expected value, and one can think of $\text{Cov}_t(f, g)$ as a ‘sample covariance’ rather than a ‘real covariance’ between random variables.

Definition 2.7. With use of the previous definition, we can define relative fitness w_a^b as follows as shorthand notation:

$$w_a^b(i) \equiv W_a^b(i) / \bar{W}_a^b. \tag{2.6}$$

Note that the average fitness is simply the population growth factor, i.e. $\bar{W}_a^b = N_b / N_a$. This can be verified by using the shortly introduced lemma 2.10 by filling in $f \equiv 1$.

Replicators can have more different characteristics than previously described. For example, if our replicators are bacteria, then we may be interested in their size, or their production of certain chemicals, or the absence or presence of certain genes, etc. The following definition of *phenotype* ϕ provides a framework to describe all of these 1-dimensional properties.

Definition 2.8. Every replicator is associated with a certain phenotype ϕ , with $\phi \in \mathbb{R}$. The phenotype of replicator i is denoted as ϕ_i . The average phenotype at time t is denoted as $\bar{\phi}_t$.

If we are interested in, say, the production of some chemical by bacteria, then we may define ϕ to be the rate at which that chemical is produced. If we are merely interested in the absence or presence of a certain gene, then we may define $\phi = 1$ for every bacteria that has the gene and $\phi = 0$ for every bacteria that does not. Throughout this thesis, we will never specify what kind of phenotype we are using, so our results apply generally to any trait that can be described using elements of \mathbb{R} .

After all these definitions, it is time for our first theorem. The following theorem was introduced by Price [1].

Theorem 2.9. *Let $a < b$, $a, b \in I$. If all children have the same phenotype as their ancestors (which we will call the assumption of faithful transmission), then*

$$\text{Cov}_a(\phi, w_a^b) = \bar{\phi}_b - \bar{\phi}_a. \tag{2.7}$$

This equation can be intuitively understood; if ϕ positively (negatively) covaries with fitness, then replicators with a higher value of ϕ will tend to be fitter (less fit) on average, so one expects the average value of ϕ to increase (decrease). Before we can formally prove the validity of equation 2.7, we will first have to introduce a lemma. This lemma will be used throughout this thesis.

Lemma 2.10. *Let $a < b$, $a, b \in I$. For any function $f(i)$ of a replicator i , the following equality holds.*

$$\sum_{i \in R_a} f(i) W_a^b(i) = \sum_{j \in R_b} f(\text{anc}_a(j)). \quad (2.8)$$

Proof. The lemma follows from definitions 2.3:

$$\begin{aligned} \sum_{i \in R_a} f(i) W_a^b(i) &= \sum_{i \in R_a} f(i) |j \in R_b : \text{anc}_a(j) = i| \\ &= \sum_{i \in R_a} \sum_{j \in R_b : \text{anc}_a(j) = i} f(i) \\ &= \sum_{i \in R_a} \sum_{j \in R_b : \text{anc}_a(j) = i} f(\text{anc}_a(j)) \\ &(\text{since } \text{anc}_a(j) : S_b \rightarrow S_a \text{ is well-defined}) = \sum_{j \in R_b} f(\text{anc}_a(j)). \end{aligned} \quad (2.9)$$

□

Now we can prove theorem 2.9.

Proof. (of theorem 2.9)

$$\begin{aligned} \text{Cov}_a(\phi, w_a^b) &= \mathbf{E}_a(\phi_i W_a^b(i) / \overline{W_a^b}) - \mathbf{E}_a(W_a^b(i) / \overline{W_a^b}) \mathbf{E}_a(\phi_i) \\ &= \sum_{i \in R_a} \frac{\phi_i W_a^b(i) / \overline{W_a^b}}{N_a} - 1 \cdot \overline{\phi_a} \\ &= \sum_{i \in R_a} \frac{\phi_i W_a^b(i)}{N_a \cdot N_b / N_a} - \overline{\phi_a} \\ &= \frac{\sum_{i \in R_a} \phi_i W_a^b(i)}{N_b} - \overline{\phi_a}. \end{aligned} \quad (2.10)$$

Lemma 2.10 implies the following.

$$\sum_{i \in R_a} \phi_i W_a^b(i) = \sum_{j \in R_b} \phi_{\text{anc}_a(j)}. \quad (2.11)$$

Also, the following is true by our assumption of faithful inheritance.

$$\phi_{\text{anc}_a(j)} = \phi_j. \quad (2.12)$$

This means that we can continue our calculation from equation 2.10 as follows.

$$\begin{aligned} \text{Cov}_a(\phi, w_a^b) &= \frac{\sum_{j \in R_b} \phi_j}{N_b} - \overline{\phi_a} \\ &= \overline{\phi_b} - \overline{\phi_a}. \end{aligned} \quad (2.13)$$

□

Under less ideal conditions, this equation does not hold. Two examples of less ideal conditions are:

- (1). Not every child needs to have the same phenotype as its ancestor. If there is a difference between the phenotype of child and ancestor, we say that an imperfect transmission has occurred. One can think of this as a mutation, but it does not need to be in general. Other factors than mutation can influence phenotype.
- (2). Not every replicator needs to have an ancestor in the population: it could have immigrated from another population. Also, not every replicator who is no longer in the population needs to have died: it could have emigrated to another population.

We will postpone discussing (2) until section 8. When we account for (1) (so we no longer assume that children have the same phenotype as their parents), we will need two terms to describe change in average phenotype: one describing the effects of selection and one describing the effects of imperfect transmission. They are introduced below.

Definition 2.11. Our old expression for change in average phenotype is called the *selection term* S_a^b :

$$S_a^b \equiv \text{Cov}_a(\phi, w_a^b). \quad (2.14)$$

The selection term seems to describe what people intuitively mean when they say that a trait or phenotype is ‘selected’ for. After all, if replicators with a higher value of some phenotype ϕ tend to have a higher fitness, one would say that this phenotype is selected for; and indeed, if this is the case the covariance between this phenotype and fitness is positive.

Definition 2.12. The following is called the *transmission term* μ_a^b :

$$\mu_a^b \equiv \mathbf{E}_b(\phi_j - \phi_{\text{anc}_a(j)}). \quad (2.15)$$

The transmission term represents the average difference between the phenotype of descendants and ancestors. For example, if at some point children tend to be longer than their parents, average population length will increase without the need for selection; and in this case, the transmission term will reflect this change in average length.

The previous two terms are used in the *Price Equation* [1]:

Theorem 2.13. (*Price Equation*)

$$\overline{\phi}_b - \overline{\phi}_a = S_a^b + \mu_a^b. \quad (2.16)$$

We can prove the Price Equation (equation 2.16) as follows.

Proof.

$$\begin{aligned} S_a^b + \mu_a^b &= \text{Cov}_a(\phi, w_a^b) + \frac{\sum_{j \in R_b} (\phi_j - \phi_{\text{anc}_a(j)})}{N_b} \\ \text{(by equations 2.10 and 2.11)} &= \frac{\sum_{j \in R_b} \phi_{\text{anc}_a(j)}}{N_b} - \overline{\phi}_a + \frac{\sum_{j \in R_b} (\phi_j - \phi_{\text{anc}_a(j)})}{N_b} \\ &= \frac{\sum_{j \in R_b} \phi_j}{N_b} - \overline{\phi}_a \\ &= \overline{\phi}_b - \overline{\phi}_a. \end{aligned} \quad (2.17)$$

□

In the literature the transmission term is most often defined in a different but equivalent way [?]. I will now show this definition by making use of notation that I have previously defined.

Definitions 2.14. Let $a < b$, $a, b \in I$ and let

$$U_i \equiv \{j \in S_b : i = \text{anc}_a(j)\} \quad (2.18)$$

be the set of replicators at time b that add to the fitness of a replicator i living at time a , which we use to define

$$\Delta\phi_i \equiv \frac{1}{W_a^b(i)} \sum_{j \in U_i} (\phi_j - \phi_i) \quad (2.19)$$

as the average change in phenotype between i and its descendants. We define the following as transmission.

$$\mu_a^{b'} \equiv \mathbf{E}_a(w_a^b \Delta\phi). \quad (2.20)$$

Theorem 2.15. *Our two definitions of transmission are equivalent, i.e., $\mu_a^{b'} = \mu_a^b$.*

Proof.

$$\begin{aligned}
\mathbf{E}_a(w_a^b \Delta \phi) &= \frac{1}{N_a} \sum_{i \in R_a} w_a^b(i) \Delta \phi_i \\
&= \frac{1}{N_a \overline{W_a^b}} \sum_{i \in R_a} W_a^b(i) \Delta \phi_i \\
&= \frac{1}{N_b} \sum_{i \in R_a} W_a^b(i) \Delta \phi_i \\
&= \frac{1}{N_b} \sum_{i \in R_a} W_a^b(i) \frac{1}{W_a^b(i)} \sum_{j \in U_i} (\phi_j - \phi_i) \\
&= \frac{1}{N_b} \sum_{i \in R_a} \sum_{j \in U_i} (\phi_j - \phi_i) \\
&= \frac{1}{N_b} \sum_{i \in R_a} \sum_{j \in U_i} (\phi_j - \phi_{\text{anc}_a(j)}) \\
&= \frac{1}{N_b} \sum_{j \in R_b} (\phi_j - \phi_{\text{anc}_a(j)}) \\
&= \mathbf{E}_b(\phi_j - \phi_{\text{anc}_a(j)}).
\end{aligned} \tag{2.21}$$

□

3 The meaning of the selection term

It is very useful to get a good grasp of what the selection and transmission terms precisely mean. Many people have an intuitive notion of selection and assume that the selection term in the Price Equation coincides with their intuition. In this section I will challenge this notion. The selection term S_a^b *only* tells you how the phenotype of replicators at time a covaries with the size of their line of descendents at time b , and I claim this differs considerably from the notion of most people of what ‘selection’ means. I will illustrate this with an example.

Example 2. Suppose $a < t_1 < t_2 < t_3 < t_4 < b$, all of which represents times. At time a there is 1 replicator with phenotype ϕ . At time t_1 it gets a child with phenotype $\phi - \epsilon$, with $\epsilon > 0$, due to a mutation. At time t_2 , the child dies. At time t_3 , the original replicator gets another child. This time, the child has phenotype $\phi + \epsilon$, meaning another mutation has occurred, but this time in the other direction. At time t_4 , the original replicator dies. As such, at time b , the child with phenotype $\phi + \epsilon$ is the only child alive. See figure 2 for a visual representation.

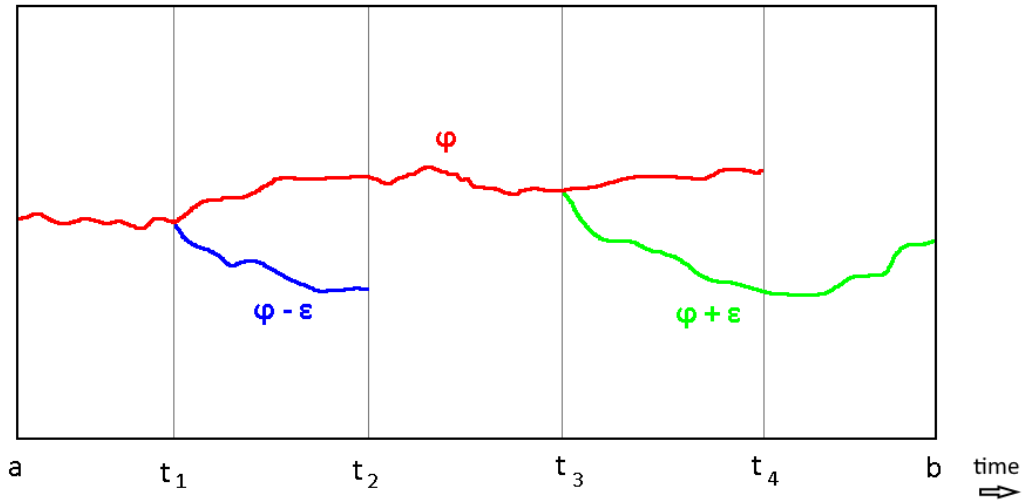


Figure 2: Example

In this situation, what would we expect the selection and transmission terms to be? Since there were two mutations of the same size but in opposite directions, should we not expect the transmission term to be zero? Since both times a replicator died, it was the replicator with the lowest phenotype in the population, should we not expect the selection term to be positive? Let us calculate the terms. It is very straightforward. Since there was only one replicator alive at time $t = a$, the covariance term has to be 0, and so

$$S_a^b = 0, \quad (3.1)$$

but evidently,

$$\bar{\phi}_b - \bar{\phi}_a = \phi + \epsilon - \phi = \epsilon > 0, \quad (3.2)$$

and so

$$\mu_a^b = \bar{\phi}_b - \bar{\phi}_a - S_a^b = \epsilon > 0. \quad (3.3)$$

According to the Price Equation, all of the change in average phenotype was due to a positive transmission term, and selection played no role. This is likely to be in contrast with our intuition of what ‘selection’ means. The reason for this discrepancy is that a lot of what happened in between times a and b is not factored into the selection term S_a^b . The phenotype of the children, for example, did not matter at all for the selection term; only the phenotype of the parent did. In addition, the birth and death of the child with phenotype $\phi - \epsilon$ was not factored into the selection term at all.

Individual intermediate events become less important when more events are happening. One may have the intuition that with more events, our intuition would get closer to the mathematics of the Price Equation. I think the opposite is true; the more intermediate events there are, the more intermediate events are not factored in the selection term, which can cause intuition to drift even further away from the mathematical meaning of the selection term. I will provide another example.

Example 3. Suppose that at time a there are two replicators. One of them has phenotype ϕ and the other has a lower phenotype of $\phi - \epsilon$. Both replicators leave offspring, but the child of the replicator with the lower phenotype of $\phi - \epsilon$ has a mutation, and as a result it gets the highest phenotype in the population of $\phi + \epsilon$. This child then proceeds to take over the entire population so that at time b , all replicators have phenotype $\phi + \epsilon$. We may think that this means that there is selection in favor of high values of phenotype, but the selection term S_a^b is actually *negative*, for the entire population of time b is a descendant of a replicator with a *low* phenotype of $\phi - \epsilon$ at time a . See figure 3 for an illustration.

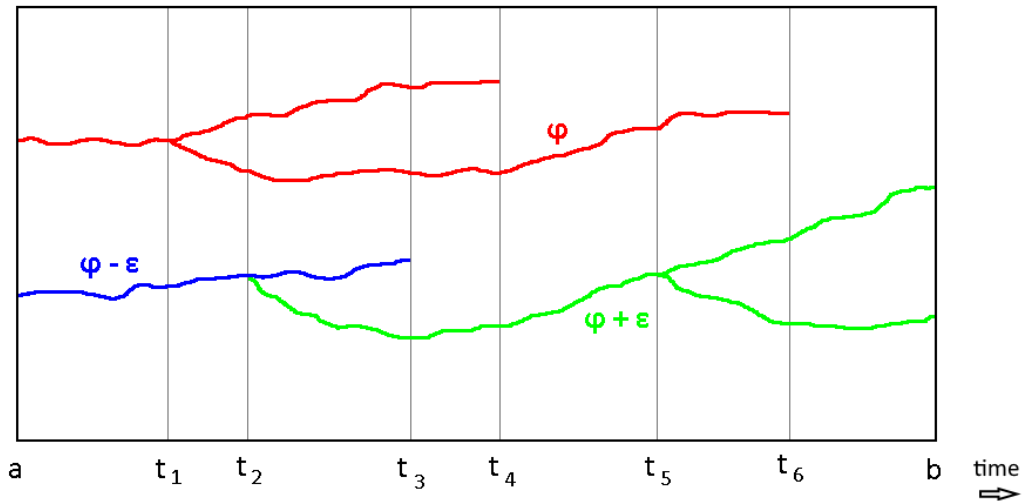


Figure 3: A replicator with a low phenotype reproduces and gets a child with a high phenotype, who then takes over the entire population.

One might argue that the Price Equation is simply not meant to be taken over too large time intervals and that one ought to not use it for a time interval that is longer than 1 generation. My response to this is that even if the selection term describes 1 generation, it can still be very counterintuitive, as our example from figure 2 shows. In addition, if it is true that the Price Equation is not meant for time intervals that are too large, this

implies that we should use another definition to be able to talk about selection on larger time scales.

I argue that the Price Equation and the corresponding selection term *are* useful on all time scales, but that we should be cautious about their interpretation. The Price Equation and its selection term seem to not capture what many people mean when they talk about selection. As such, I argue that it would be useful to make an extra definition that *does* correspond with people's intuition. If such a definition would be found, it would provide a useful addition to our toolbox to talk about selection.

4 Searching for a new definition of selection

In order to find useful new definitions of selection that intuitively describe how selection influences change in average phenotype, we will first write down the selection term of the Price Equation in terms of individual births and deaths.

Definition 4.1. The event in which a replicator reproduces we will call a replication event and the event in which a replicator dies we will call a death event.

Let x be a replication or death event and let $i(x)$ be the replicator replicating or dying in birth or death event x . Let f be a function of replicators. Whenever we write $f(x)$, it means $f(i(x))$. We will often explicitly mention it whenever we abuse notation this way.

Lemma 4.2. Let r_1, r_2, \dots, r_n be the replication events in the time interval $(a, b]$ and let d_1, d_2, \dots, d_m be the death events in the time interval $(a, b]$. With $\text{anc}_a(r_i)$ and $\text{anc}_a(d_j)$ we refer to the replicator at time a that is the ancestor of the replicator reproducing in replication event r_i or dying in death event d_j , respectively. Then

$$S_a^b = \frac{1}{N_b} \left(\sum_{i=1}^n \phi_{\text{anc}_a(r_i)} - \sum_{j=1}^m \phi_{\text{anc}_a(d_j)} + (N_a - N_b) \overline{\phi_a} \right). \quad (4.1)$$

Proof. Let $R_a = \{a_1, a_2, \dots, a_{N_a}\}$ be the set of replicators alive at time a . Let $C_{a_k}^b$ be the set of replication events in the lineage of replicator k in the time interval $(a, b]$ and let $D_{a_k}^b$ be the set of death events in the lineage of replicator k in the time interval $(a, b]$. Notice that $W_a^b(k) = 1 + |C_{a_k}^b| - |D_{a_k}^b|$. Then

$$\begin{aligned} S_a^b &= \text{Cov}(\phi, w_a^b) \\ \text{(by equation 2.10)} &= \frac{\sum_{k \in R_a} \phi_k W_{a_k}^b}{N_b} - \frac{\sum_{k \in R_a} \phi_k}{N_a} \\ &= \frac{\sum_{k \in R_a} \phi_k (1 + |C_{a_k}^b| - |D_{a_k}^b|)}{N_b} - \frac{\sum_{k \in R_a} \phi_k}{N_a} \\ &= \frac{\sum_{k \in R_a} \phi_k (|C_{a_k}^b| - |D_{a_k}^b|)}{N_b} + \frac{\sum_{k \in R_a} \phi_k}{N_b} - \frac{\sum_{k \in R_a} \phi_k}{N_a} \\ &= \frac{\sum_{k \in R_a} \phi_k (\sum_{r_i \in C_{a_k}^b} 1 - \sum_{d_j \in D_{a_k}^b} 1)}{N_b} + \frac{N_a \sum_{k \in R_a} \phi_k}{N_a N_b} - \frac{N_b \sum_{k \in R_a} \phi_k}{N_a N_b} \\ &= \frac{\sum_{k \in R_a} (\sum_{r_i \in C_{a_k}^b} \phi_k - \sum_{d_j \in D_{a_k}^b} \phi_k)}{N_b} + \frac{N_a \sum_{k \in R_a} \phi_k}{N_a N_b} - \frac{N_b \sum_{k \in R_a} \phi_k}{N_a N_b} \\ &= \frac{\sum_{k \in R_a} (\sum_{r_i \in C_{a_k}^b} \phi_{\text{anc}_a(r_i)} - \sum_{d_j \in D_{a_k}^b} \phi_{\text{anc}_a(d_j)})}{N_b} + \frac{(N_a - N_b) \sum_{k \in R_a} \phi_k}{N_a N_b} \\ &= \frac{\sum_{i=1}^n \phi_{\text{anc}_a(r_i)} - \sum_{j=1}^m \phi_{\text{anc}_a(d_j)}}{N_b} + \frac{(N_a - N_b) \overline{\phi_a}}{N_b} \\ &= \frac{1}{N_b} \left(\sum_{i=1}^n \phi_{\text{anc}_a(r_i)} - \sum_{j=1}^m \phi_{\text{anc}_a(d_j)} + (N_a - N_b) \overline{\phi_a} \right). \end{aligned} \quad (4.2)$$

□

We will introduce a new definition of selection, $S_a^{b'}$, in which for every birth or death event, we use the phenotype of the replicator that gives birth or dies, instead of the phenotype of the ancestral replicator. We do this as follows.

Definition 4.3. Let ϕ_{r_i} be the phenotype of the replicator that reproduces in birth event r_i and let ϕ_{d_j} be the phenotype of the replicator that dies at death event d_j . Then we define

$$S_a^{b'} \equiv \frac{1}{N_b} \left(\sum_{i=1}^n \phi_{r_i} - \sum_{j=1}^m \phi_{d_j} + (N_a - N_b) \overline{\phi}_a \right). \quad (4.3)$$

This is the analogue to equation 4.1 were we use the phenotype of the replicators that give birth or die, as opposed to the phenotype of their ancestor.

The main reason why the term S_a^b is not in accordance to what many people intuitively mean with ‘selection’ seems to be that in this term, whenever a replicator reproduces or dies, the only thing that counts is the phenotype of its ancestor at time a , rather than its own phenotype. The new definition of $S_a^{b'}$ solves this problem. Our hope is that $S_a^{b'}$ is better at describing our intuition on selection than S_a^b is. In case ϕ is faithfully inherited, i.e. every child has the same phenotype as its parent, S_a^b captures the full change in average phenotype, in accordance to what we would expect intuitively. This was shown in theorem 2.9. It would be nice if the same were true for $S_a^{b'}$.

Theorem 4.4. *If ϕ is faithfully inherited, then*

$$S_a^{b'} = S_a^b = \overline{\phi}_b - \overline{\phi}_a. \quad (4.4)$$

Because of the way we have constructed $S_a^{b'}$, we can expect this to be indeed the case. We will now formally show this.

Proof. Under the assumption of faithful inheritance, for all replication events r_i and death events d_j , $\phi_{r_i} = \phi_{\text{anc}_a(r_i)}$ and $\phi_{d_j} = \phi_{\text{anc}_a(d_j)}$. From this fact follows that $S_a^{b'} = S_a^b$. Theorem 2.9 states that under the assumption of faithful inheritance, $S_a^b = \overline{\phi}_b - \overline{\phi}_a$. Hence also $S_a^{b'} = \overline{\phi}_b - \overline{\phi}_a$. \square

More generally, if every replicator that reproduces or dies in between $t = a$ and $t = b$ can be traced back to an ancestor that carries the same phenotype, the definitions $S_a^{b'}$ and S_a^b agree with each other. The simple reason is that in this case, $S_a^{b'}$ as defined in equation 4.3 precisely coincides with the term that we end up with in equation 4.2.

Let us now look at what our definition says in example 2 on page 10. We have

$$\begin{aligned} S_a^{b'} &= \frac{1}{1} (2\phi - (\phi + (\phi - \epsilon)) + (1 - 1)\phi) \\ &= \epsilon, \end{aligned} \quad (4.5)$$

so the selection term of $S_a^{b'}$ accounts for the full change in average phenotype. This seems to align with our intuition of what it means to have selection within a time interval more so than the term S_a^b does.

Now let us take a look at another example.

Example 4. Suppose that at time a , there are two replicators, both with phenotype ϕ . At time t_1 , one of them reproduces and produces a mutant with phenotype $\phi + \epsilon$. At time t_2 , the other one dies. These are the only events that happen in the time interval $(a, b]$. See figure 4 for a representation where first $t_1 < t_2$ and then $t_1 > t_2$.

In both of these examples there is no difference in phenotype in the initial replicators, so

$$S_a^b = 0. \quad (4.6)$$

Also in these examples, we have

$$\begin{aligned} S_a^{b'} &= \frac{1}{2} (\phi - \phi + (2 - 2)\phi) \\ &= 0. \end{aligned} \quad (4.7)$$

This result seems to make sense for the case where $t_1 > t_2$. In this case, every birth and death event happened at a point in time where every replicator in the population had the exact same phenotype, so there *could* not have been any selection! If $t_1 < t_2$, the situation is different, though. Here, the death of a replicator with phenotype ϕ happened at a moment in time where its phenotype was lower than the population average, as the

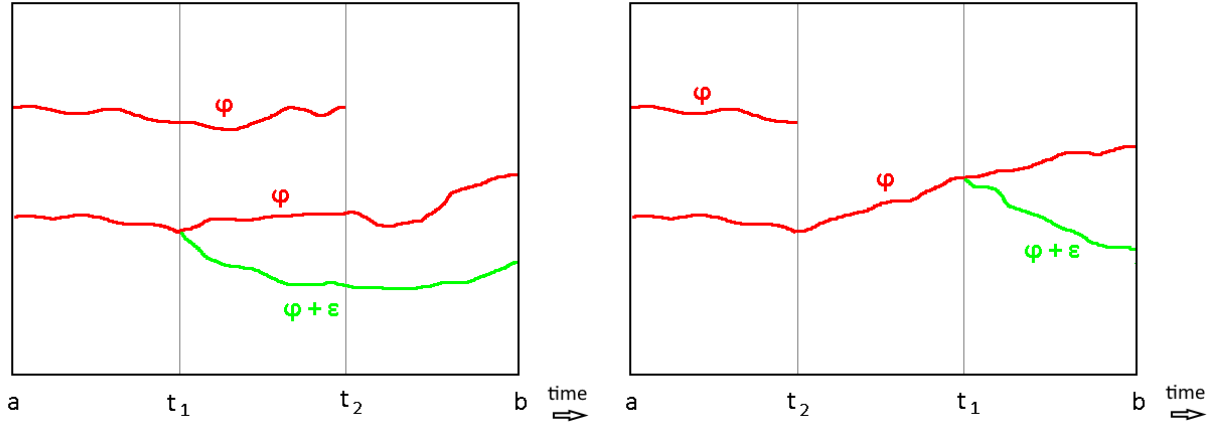


Figure 4: Another example. Left: $t_1 < t_2$. Right: $t_1 > t_2$.

replicator with phenotype $\phi + \epsilon$ had already been born. Hence in this case, the death resulted in an increase of average phenotype, and so one could argue that the death of this replicator was an example of selection in favor of higher values of the phenotype. This is not captured in the term $S_a^{b'}$, though. The term $S_a^{b'}$ could not capture this, as it does not factor in the time of the events; if one changes the order of two events (so long as one *could* change the order; a parent cannot give birth before it is born itself), $S_a^{b'}$ remains unchanged. As such, it *cannot* make any distinction between the case where $t_1 > t_2$ and the case where $t_1 < t_2$. This is maybe not desirable and we will continue our search for a new definition of selection.

5 An order-dependent definition of selection

Previously, we saw that the selection term gets muddled with effects from transmission if one looks at selection at larger time scales. One solution for this is to ‘cut’ time into smaller pieces. As an example, suppose we are interested in the influence of selection between $t = 0$ and $t = 10$. We are worried that the selection term S only captures the effects of selection well on time scales no larger than 1. Then instead of using the term S_0^{10} to describe the effects of selection between $t = 1$ and $t = 10$, we could decide to use the term $S_0^1 + S_1^2 + \dots + S_9^{10}$ instead. This example leads us to a new definition.

Definition 5.1. Let $a, b \in I$, $a < b$, and let $k \in \mathbb{N}$. We write $j \equiv \frac{a-b}{k}$ and define the following.

$$S_a^{b,k} \equiv \sum_{s=0}^{k-1} S_{a+s}^{a+(s+1)j} = \sum_{s=0}^{k-1} \text{Cov}_a(\phi, w_{a+s}^{a+(s+1)j}). \quad (5.1)$$

In this definition, we calculate selection in between $t = a$ and $t = a + kj$, but we do so by adding k different selection terms that look at selection at time lengths of j . Using our previous example, the term $S_0^1 + S_1^2 + \dots + S_9^{10}$ can be written simply as $S_0^{10,10}$; we go from $t = 0$ to $t = 10$ in 10 steps.

Theorem 5.2. *If the phenotype is faithfully inherited, then for all $j \in \mathbb{R}, k \in \mathbb{N}$ with $kj = b - a$,*

$$S_a^{b,k} = S_a^b. \quad (5.2)$$

This can be easily shown as follows.

Proof. Remember $j \equiv \frac{b-a}{k}$. If ϕ is faithfully inherited, the transmission term over any time interval will be equal to 0, and hence we have

$$\begin{aligned}
S_a^{b,k} &= \sum_{s=0}^{k-1} S_{a+s}^{a+(s+1)j} \\
&= \sum_{s=0}^{k-1} (\overline{\phi_{a+(s+1)j}} - \overline{\phi_{a+s}}) \\
&= \overline{\phi_{a+k}} - \overline{\phi_a} \\
&= \overline{\phi_b} - \overline{\phi_a} \\
&= S_a^b.
\end{aligned} \tag{5.3}$$

□

6 The limit definition of selection

With help of our definition $S_a^{b,k}$, we can study selection at any time scale. We could ask ourselves whether it is always better to look at selection on smaller scales. In the term $S_a^{b,10}$ the selection and transmission term are less mixed up than in the term S_a^b . But we may expect the selection and transmission term to be even less intertwined in the term $S_a^{b,100}$, and even less in the term $S_a^{b,1000}$. We could go on with this forever. What if we make k arbitrarily large and use $j \equiv \frac{b-a}{k}$ *infinitesimally* small timesteps? Consider the following definition.

Definition 6.1.

$$S_a^b \equiv \lim_{k \uparrow \infty} S_a^{b,k}. \tag{6.1}$$

Most of the terms in our summation would be 0, since in most very small time intervals, no birth or death occurs. We would just be counting birth and deaths, like we did in the definition of $S_a^{b'}$, except that the time of the events is taken into consideration. How would this look like? We will first need to introduce new notation.

Definition 6.2. Let $f(t)$ be any property that is a function of time. We write

$$f^-(t) \equiv \lim_{\epsilon \downarrow 0} f(t - \epsilon). \tag{6.2}$$

We will often make explicit whenever we make use of this definition.

Now we are ready for the theorem.

Theorem 6.3. Let $a < b$. Let r_1, r_2, \dots, r_n be the birth events in the time interval $(a, b]$, let d_1, d_2, \dots, d_m be the death events in the time interval $(a, b]$, let ϕ_{r_i} be the phenotype of the replicator reproducing in replication event r_i , let ϕ_{d_j} be the phenotype of the replicator dying in replication event d_j , and let t_i, t_j be the respective times of replication event r_i and death event d_j . Furthermore, using definition ??, we write $\overline{\phi_t^-} \equiv \lim_{\epsilon \downarrow 0} \overline{\phi_{t-\epsilon}}$. Then

$$S_a^b = \sum_{i=1}^n \frac{\phi_{r_i} - \overline{\phi_{t_i^-}}}{N_{t_i}} + \sum_{j=1}^m \frac{\overline{\phi_{t_j^-}} - \phi_{d_j}}{N_{t_j}}. \tag{6.3}$$

The proof can be found in section A of the appendix.

We will now take a look at some examples to get a better intuitive understanding of the differences between the terms we have found so far.

If ϕ is faithfully inherited, then $S_a^b = S_a^b$ for the simple reason that $S_a^{b,k} = S_a^b$ for all k if ϕ is faithfully inherited. In general, $S_a^b \neq S_a^b$, though. To show this, consider again example 2 on page 10. Remember that in this example,

$$\overline{\phi_b} - \overline{\phi_a} = \epsilon, \tag{6.4}$$

but

$$S_a^b = 0. \tag{6.5}$$

Our new definition gives

$$\begin{aligned}
S_a^b &= \frac{\phi - \phi}{2} + \frac{(\phi + \phi - \epsilon)/2 - (\phi - \epsilon)}{1} + \frac{\phi - \phi}{2} + \frac{(\phi + \phi + \epsilon)/2 - \phi}{1} \\
&= \frac{\phi + \phi - \epsilon}{2} - (\phi - \epsilon) + \frac{\phi + \phi + \epsilon}{2} - \phi \\
&= \frac{\epsilon}{2} + \frac{\epsilon}{2} \\
&= \epsilon,
\end{aligned} \tag{6.6}$$

so this new selection term does account for the full change in average phenotype, just like $S_a^{b'}$ does.

Now let us return to example 4 on page 13. Suppose that $t_1 < t_2$. In that case,

$$\begin{aligned}
S_a^b &= \frac{1}{3}(\phi_0 - \phi) + \frac{1}{2}\left(\frac{\phi + \phi + \phi + \epsilon}{3} - \phi\right) \\
&= \frac{\epsilon}{6},
\end{aligned} \tag{6.7}$$

but if $t_1 > t_2$, then

$$\begin{aligned}
S_a^b &= \frac{1}{1}(\phi - \phi) + \frac{1}{2}(\phi - \phi) \\
&= 0,
\end{aligned} \tag{6.8}$$

which yields a different result. Our new definition does capture the difference between the situations where $t_1 < t_2$ and where $t_1 > t_2$. The results make sense, too: if $t_1 < t_2$, the death event will directly cause the average phenotype to increase by a factor $\frac{\epsilon}{6}$, but if $t_1 > t_2$, the death event has no immediate effect on average phenotype.

Interestingly, $S_a^{b'}$ agrees with S_a^b if the order of events is like in equation 6.8 but not if the order of events is like in equation 6.7. One intuitive way of looking at this is the following. The reason why the selection term is positive in equation 6.7 is because if $t_1 < t_2$, the death of the replicator carrying phenotype ϕ happens at a time where the value of its phenotype was lower than the population average. In equation 6.8, on the other hand, the death event happens at a moment in time where the dying replicator carries the average phenotype. The term $S_a^{b'}$ can be interpreted as selection in a world where there is no order of events, i.e. ‘everything happens simultaneously’. If the birth and death events happen simultaneously, then the birth of the mutant with phenotype $\phi + \epsilon$ and the death of the replicator with phenotype ϕ cannot be causally linked. Hence we can ignore the birth event in determining the effects on selection of the death event, and when we do so, the dying replicator has an average phenotype at the moment of its death.

7 New definitions of transmission

So far, we have only focused on the selection term. We would like to study the transmission term, too. We have made some different definitions of selection. In order for the Price Equation to hold for these new definitions, we need to also invent new analogous definitions for transmission. These analogous definitions will be introduced in this section.

Remark 7.1. We are continuously assuming that imperfect transmission only takes place during reproduction, i.e., it treats the phenotype of replicators during their lifetime as constant. This seems like a very narrow view. Luckily, it is not very difficult to extend all of our theorems to include the possibility of phenotype changing spontaneously. If a replicator changes its phenotype at some moment in time t , one can mathematically treat the situation as if the replicator died at time t and at the exact same time gave birth to a new replicator that carries a different phenotype. This has no effect on the selection term, since these birth and death events cancel each other out, resulting in no net change in fitness. Note that this extension is only made possible by the fact that our replicators live in halfopen intervals. To illustrate this, suppose a replicator i dies and gives birth to another replicator at time t , and suppose that $s < t$. If replicators lived in closed intervals, $W_s^t(i)$ would be 1 number higher than it should be (since at time t , both replicators would exist, and if replicators lived in open intervals, it would be 1 number lower (since at time t , neither replicator would exist).

Only when phenotype changes continuously instead of discretely, some of our theorems would no longer work or should be written in a more sophisticated way.

To recap,

$$S_a^{b'} \equiv \frac{1}{N_b} \left(\sum_{i=1}^n \phi_{r_i} - \sum_{j=1}^m \phi_{d_j} + (N_a - N_b) \overline{\phi_a} \right). \quad (7.1)$$

Definition 7.2. Let $\Delta\phi_{r_i}$ be the phenotype of the child in reproduction event r_i minus the phenotype of its parent. Then we define

$$\mu_a^{b'} \equiv \frac{1}{N_b} \sum_{i=1}^n \Delta\phi_{r_i}. \quad (7.2)$$

Theorem 7.3.

$$\overline{\phi_b} - \overline{\phi_a} = S_a^{b'} + \mu_a^{b'}. \quad (7.3)$$

This can be proven as follows.

Proof. Let $R_a = \{a_1, a_2, \dots, a_{N_a}\}$ and $R_b = \{b_1, b_2, \dots, b_{N_b}\}$. Using the same notation as in equation ?? (e.g. n and m are the number of birth and death events in $(a, b]$, respectively) and largely following the same steps as in this equation, we calculate the following.

$$\begin{aligned} \overline{\phi_b} - \overline{\phi_a} &= \frac{1}{N_b} \left(\sum_{k=1}^{N_b} \phi_{b_k} \right) - \overline{\phi_a} \\ &= \frac{1}{N_b} \left(\sum_{l=1}^{N_a} \phi_{a_l} + \sum_{i=1}^n (\phi_{r_i} + \Delta\phi_{r_i}) - \sum_{j=1}^m \phi_{d_j} \right) - \overline{\phi_a} \\ &= \frac{1}{N_b} (N_a \overline{\phi_a} + \sum_{i=1}^n \phi_{r_i} - \sum_{j=1}^m \phi_{d_j}) - \overline{\phi_a} + \frac{1}{N_b} \sum_{i=1}^n \Delta\phi_{r_i} \\ &= \frac{1}{N_b} \left(\sum_{i=1}^n \phi_{r_i} - \sum_{j=1}^m \phi_{d_j} + N_a \overline{\phi_a} - N_b \overline{\phi_a} \right) + \mu_a^{b'} \\ &= \frac{1}{N_b} \left(\sum_{i=1}^n \phi_{r_i} - \sum_{j=1}^m \phi_{d_j} + (N_a - N_b) \overline{\phi_a} \right) + \mu_a^{b'} \\ &= S_a^{b'} + \mu_a^{b'}. \end{aligned} \quad (7.4)$$

□

Now we will find our transmission term in the definition of $S_a^{b,k}$. We define

Definition 7.4.

$$\mu_a^{b,k} \equiv \sum_{s=0}^{k-1} \mu_{a+s_j}^{a+(s+1)j}, \quad (7.5)$$

which is analogous to the definition of $S_a^{b,k}$.

Theorem 7.5.

$$S_a^{b,k} + \mu_a^{b,k} = \overline{\phi_b} - \overline{\phi_a}. \quad (7.6)$$

Proof. This proof takes only a few steps.

$$\begin{aligned} S_a^{b,k} + \mu_a^{b,k} &= \sum_{s=0}^{k-1} S_{a+s_j}^{a+(s+1)j} + \sum_{s=0}^{k-1} \mu_{a+s_j}^{a+(s+1)j} \\ &= \sum_{s=0}^{k-1} (S_{a+s_j}^{a+(s+1)j} + \mu_{a+s_j}^{a+(s+1)j}) \\ &= \sum_{s=0}^{k-1} (\overline{\phi_{a+(s+1)j}} - \overline{\phi_{a+s_j}}) \\ &= \overline{\phi_b} - \overline{\phi_a}. \end{aligned} \quad (7.7)$$

□

Next, we will focus our attention to $\lim_{k \uparrow \infty} \mu_a^{b,k}$. We define it as follows.

Definition 7.6. $U_a^b \equiv \lim_{k \uparrow \infty} \mu_a^{b,k}$.

Theorem 7.7. Let r_1, r_2, \dots, r_n be all the birth events in the time interval $(a, b]$, let $\Delta\phi_{r_i}$ be the phenotype of the parent minus that of the child in reproduction event r_i , and let t_i be the time that replication event r_i occurs. Then

$$U_a^b = \sum_{i=1}^n \frac{\Delta\phi_{r_i}}{N_{t_i}}. \quad (7.8)$$

See Appendix B for a (summary of) the proof.

8 Migration and the local Price Equation

There is another way in which the average phenotype of a population can change that we have not focused on so far: migration. This section is devoted to developing a framework to describe locality and migration in a general way. Note that if we use a migration term, we are necessarily looking at a local environment or local population of replicators. As such, if we add a migration term to the Price Equation, we will call it the *local Price Equation*. We will also talk about corresponding *local selection* and *local transmission*.

There are various ways to describe migration mathematically. Previously when we briefly discussed migration, we talked about migration as the effects of replicators entering (immigration into) and leaving (emigrating out of) a population. When talking about it this way, we either consider replicators to be inside or outside our local environment. One can imagine situations, though, in which we may need a description that is less black-and-white; e.g., we may want to count replicators near the boundary of our local environment as being ‘half inside’ and ‘half outside’. The following definition is chosen with this in mind.

Definition 8.1. Let $I \subseteq \mathbb{R}$ and let $K : (i, \tau)_{i \in R_\tau, \tau \in I} \rightarrow \mathbb{R}$ be a function that describes how much each replicator ‘counts’ at every point in time; i.e., for every replicator i and time τ , $K(i, \tau)$ is only defined if i is alive at time τ and is a measure for how much this replicator counts at this time. We will call K a *weight function*.

A weight function $K : (i, \tau)_{i \in R_\tau, \tau \in I} \rightarrow \mathbb{R}$ is required to satisfy the following properties. Properties 2 and 3 will only start to play a role in much later chapters and can be ignored for the moment.

1. For all $t \in I$ and $i \in R_t$

$$K(i, t) \geq 0, \quad (8.1)$$

i.e., no replicator counts ‘negatively’ for any group.

2. All left limits in time of K exist.
3. K is right continuous in time.

We will use a weight function K to model migration in a local environment. Migration occurs whenever for some replicator i , $K(i, t)$ is not constant in t . For instance, if $K(i, t)$ is decreasing in time, the replicator i is ‘migrating away’ from our local environment. Note that if the function K only takes on the values 0 and 1, then we would be back to our narrow view of replicators being either inside or outside our local environment.

In practise, one can define a spatial position of replicators and use this position in space to determine their weight K . In this case, K is a function of some space \mathcal{S} that the replicators are living in, rather than from replicators and time. However, one would need an additional function describing the position in space \mathcal{S} of each replicator at each point in time, making K indirectly a function of replicators and time.

In order to avoid clutter in the rest of this section, we will make use of the following shorthand notation.

Definition 8.2. For all replicators j , we write $K(\text{anc}_a(j)) \equiv K(\text{anc}_a(j), a)$, i.e., $K(\text{anc}_a(j))$ denotes the weight at time a of the ancestor of replicator j .

Even without migration, using this new formalism of weight functions means we have to re-write our definitions of selection and transmission. After all, selection and transmission on a replicator with a high value of K should

have a larger effect on the respective selection and transmission terms than selection and transmission on a replicator with a low value of K . Hence, where we used averages before in our definitions, we should now use averages weighted by K .

Definitions 8.3. Let $t \in I$ and let f be a real-valued function of replicators. Then we write the following.

$$\mathbf{E}_t^{(K)}(f) \equiv \bar{f}_t^{(K)} \equiv \frac{\sum_{i \in R_t} K(i, t) f(i)}{\sum_{i \in R_t} K(i, t)} \equiv \bar{f}_t. \quad (8.2)$$

Note that if $K \equiv 1$, this coincides with equation 2.4. More generally, let $s, t \in I$ and let $f : R_t \rightarrow \mathbb{R}$ and $h : R_t \rightarrow (R_s, s)$. We write the following.

$$\mathbf{E}_t^{(K)}(f|h) \equiv \frac{\sum_{i \in R_t} K(h(i)) f(i)}{\sum_{i \in R_t} K(h(i))}. \quad (8.3)$$

We will mainly use this definition for functions h in the form $h(i) = (\text{anc}_s(i), s)$, which can, inside a weight function, be shortly written as $h(i) = \text{anc}_s(i)$ when applying definition 8.2.

We have similar notation for (sample) covariance. let g be a real-valued function of replicators too. We write

$$\text{Cov}^{(K)}(f, g) = \mathbf{E}_t^{(K)}(fg) - \mathbf{E}_t^{(K)}(f)\mathbf{E}_t^{(K)}(g) \quad (8.4)$$

and

$$\text{Cov}^{(K)}(f, g|h) = \mathbf{E}_t^{(K)}(fg|h) - \mathbf{E}_t^{(K)}(f|h)\mathbf{E}_t^{(K)}(g|h). \quad (8.5)$$

With use of this notation, we can attempt to write down the terms of the local Price Equation.

Definition 8.4. We will still have the same kind of notation for the selection term:

$$S_a^{b(K)} \equiv \text{Cov}_a^{(K)}(\phi, w_a^b). \quad (8.6)$$

The only difference is that now, we are making use of definitions 8.3 for covariance and expected value.

We could choose to define our local transmission term as follows.

Definition 8.5. We define the term $\mu_a^{b(K)(1)}$ similar to our definition of μ_a^b in 2.12, except that we use definitions 8.3 for expected value.

$$\mu_a^{b(K)(1)} \equiv \mathbf{E}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)}). \quad (8.7)$$

Note that if $K \equiv 1$ (or any other constant), our definitions of S_a^b and $\mu_a^{b(K)(1)}$ coincide with our old definitions of S_a^b and μ_a^b , simply because equation 8.2 coincides with equation 2.4 if $K \equiv 1$.

Now there is only one way to define our migration term that will result in all the terms to sum up to $\bar{\phi}_b - \bar{\phi}_a$. I define the following:

Definition 8.6.

$$M_a^{b(K)(1)} \equiv \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)}) - \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)} | \text{anc}_a(j)). \quad (8.8)$$

For this, I claim that

Theorem 8.7.

$$\bar{\phi}_b - \bar{\phi}_a = S_a^{b(K)} + \mu_a^{b(K)(1)} + M_a^{b(K)(1)}. \quad (8.9)$$

In order to prove this, we will first introduce a useful lemma:

Lemma 8.8.

$$S_a^{b(K)} = \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)} | \text{anc}_a(j)) - \bar{\phi}_a^{(K)}. \quad (8.10)$$

Proof.

$$\begin{aligned}
S_a^{b(K)} &\equiv \text{Cov}_a^{(K)}(\phi, W_a^b / \overline{W_a^b}) \\
&= \mathbf{E}_a^{(K)}(\phi_i W_a^b(i) / \overline{W_a^b}^{(K)}) - \mathbf{E}_a^{(K)}(W_a^b(i) / \overline{W_a^b}^{(K)}) \mathbf{E}_a^{(K)}(\phi_i) \\
&= \frac{\sum_{i \in R_a} K(i, a) \phi_i W_a^b(i) / \overline{W_a^b}^{(K)}}{\sum_{i \in R_a} K(i, a)} - \overline{\phi}_a^{(K)} \\
&= \frac{\sum_{i \in R_a} K(i, a) \phi_i W_a^b(i) \cdot \sum_{i \in R_a} K(i, a)}{\sum_{i \in R_a} K(i, a) \cdot \sum_{i \in R_a} K(i, a) W_a^b(i)} - 1 \cdot \overline{\phi}_a^{(K)} \\
&= \frac{\sum_{i \in R_a} K(i, a) \phi_i W_a^b(i)}{\sum_{i \in R_a} K(i, a) W_a^b(i)} - \overline{\phi}_a^{(K)} \\
\text{(using lemma 2.10)} &= \frac{\sum_{j \in R_b} K(\text{anc}_a(j)) \phi_{\text{anc}_a(j)}}{\sum_{j \in R_b} K(\text{anc}_a(j))} - \overline{\phi}_a^{(K)} \\
&= \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)} | \text{anc}_a(j)) - \overline{\phi}_a^{(K)}.
\end{aligned} \tag{8.11}$$

□

Using this lemma, proving theorem 8.7 is straightforward.

Proof. Putting all previous terms together,

$$\begin{aligned}
&S_a^{b(K)} + \mu_a^{b(K)(1)} + M_a^{b(K)(1)} \\
&= \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)} | \text{anc}_a(j)) - \overline{\phi}_a^{(K)} + \mathbf{E}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)}) + \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)}) - \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)} | \text{anc}_a(j)) \\
&= -\overline{\phi}_a^{(K)} + \mathbf{E}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)}) + \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)}) \\
&= -\overline{\phi}_a^{(K)} + \mathbf{E}_b^{(K)}(\phi_j) + \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)}) - \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)}) \\
&= -\overline{\phi}_a^{(K)} + \mathbf{E}_b^{(K)}(\phi_j) \\
&= \overline{\phi}_b^{(K)} - \overline{\phi}_a^{(K)}.
\end{aligned} \tag{8.12}$$

□

We now have a local version of the Price Equation. Let us try to interpret our terms and decide whether or not we are satisfied with our definitions and results so far.

The term $M_a^{b(K)(1)}$ can be intuitively understood as the average difference between the weight of descendants and of their parents, weighted by the phenotype of the parents. There is, however, an objection to be made to our definition of terms with regards to the term $\mu_a^{b(K)(1)}$. This is surprising, since this term seems to have logically followed from our previous definition of transmission. The objection is that the term is dependent on migration effects. Suppose that we know everything about a population of replicators at time $t = a$. We also know what the fitness w_a^b of the replicators are and which imperfect transmissions will occur in the time interval $(a, b]$. With this information, we will not be able to calculate $\mu_a^{b(K)(1)}$. The reason for this is that the weight of the descendants at time b appears in the definition of $\mu_a^{b(K)(1)}$. We do not know these weights, for we do not know anything about migration. If we want to have a definition of transmission that can be calculated without knowing anything about migration, we have to work with the weight of the ancestors at time a , not of the descendants at time b . This leads us to define the following, alternative definition of local transmission.

Definition 8.9.

$$\mu_a^{b(K)(2)} \equiv \mathbf{E}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)} | \text{anc}_a(j)). \tag{8.13}$$

In case $K \equiv 1$, we can see that $\mu_a^{b(K)(2)}$ equals the term μ_a^b from definition 2.12. Therefore, $\mu_a^{b(K)(1)}$ is not a more logical extension of our previous definition of μ_a^b than $\mu_a^{b(K)(2)}$ is.

In order for everything to sum up to $\overline{\phi}_b^{(K)} - \overline{\phi}_a^{(K)}$, we now have to define our migration term differently. I define it as follows:

Definition 8.10.

$$\begin{aligned}
M_a^{b(K)(2)} &\equiv \mathbf{E}_b^{(K)}(\phi_j) - \mathbf{E}_b^{(K)}(\phi_j | \text{anc}_a(j)) \\
&= \frac{\sum_{j \in R_b} K(j)\phi_j}{\sum_{j \in R_b} K(j)} - \frac{\sum_{j \in R_b} K(\text{anc}_a(j))\phi_j}{\sum_{j \in R_b} K(\text{anc}_a(j))} \\
&= \overline{\phi}_b^{(K)} - \frac{\sum_{j \in R_b} K(\text{anc}_a(j))\phi_j}{\sum_{j \in R_b} K(\text{anc}_a(j))}.
\end{aligned} \tag{8.14}$$

I claim that this term will make the local Price Equation work:

Theorem 8.11.

$$\overline{\phi}_b^{(K)} - \overline{\phi}_a^{(K)} = S_a^{b(K)} + \mu_a^{b(K)(2)} + M_a^{b(K)(2)}. \tag{8.15}$$

Proof. We again make use of lemma 8.8.

$$\begin{aligned}
&S_a^{b(K)} + \mu_a^{b(K)(2)} + M_a^{b(K)(2)} \\
&= \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)} | \text{anc}_a(j)) - \overline{\phi}_a + \mathbf{E}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)} | \text{anc}_a(j)) + \mathbf{E}_b^{(K)}(\phi_j) - \mathbf{E}_b^{(K)}(\phi_j | \text{anc}_a(j)) \\
&= \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)} | \text{anc}_a(j)) - \overline{\phi}_a^{(K)} + \mathbf{E}_b^{(K)}(\phi_j | \text{anc}_a(j)) - \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)} | \text{anc}_a(j)) + \mathbf{E}_b^{(K)}(\phi_j) - \mathbf{E}_b^{(K)}(\phi_j | \text{anc}_a(j)) \\
&= -\overline{\phi}_a^{(K)} - \mathbf{E}_b^{(K)}(\phi_j) \\
&= \overline{\phi}_b^{(K)} - \overline{\phi}_a^{(K)}.
\end{aligned} \tag{8.16}$$

□

We now have an alternative local Price Equation with new definitions. We can, unfortunately, make a similar objection about these definitions as we made about our previous ones. Suppose that we know everything about a population of replicators at time $t = a$. We also know what the fitness w_a^b of the replicators are and how all the weights will change in the time interval $(a, b]$. With this information, we will not be able to calculate $M_a^{b(K)(2)}$. The reason for this is that the phenotype of the descendants at time b appears in the definition of $M_a^{b(K)(2)}$. We do not know these phenotypes, for we do not know anything about how perfect the transmissions were. If we want to have a definition of migration that can be calculated without knowing anything about transmission, we have to work with the phenotype of the ancestors at time a , not of the descendants at time b . Such a definition of migration we have already used; it is $M_a^{b(K)(1)}$!

Our purest definition of transmission seems to be $\mu_a^{b(K)(2)}$ and our purest definition of migration seems to be $M_a^{b(K)(1)}$. But if we add $S_a^{b(K)} + \mu_a^{b(K)(2)} + M_a^{b(K)(1)}$, we won't necessarily arrive at $\overline{\phi}_b^{(K)} - \overline{\phi}_a^{(K)}$; we will be missing something. The following definition and theorem show us what will be missing.

Definition 8.12.

$$\kappa_a^{b(K)} \equiv \mathbf{E}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)}) - \mathbf{E}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)} | \text{anc}_a(j)). \tag{8.17}$$

Theorem 8.13.

$$\overline{\phi}_b^{(K)} - \overline{\phi}_a^{(K)} = S_a^{b(K)} + \mu_a^{b(K)(2)} + M_a^{b(K)(1)} + \kappa_a^{b(K)}. \tag{8.18}$$

We can show this as follows.

Proof. We use that fact that

$$\begin{aligned}
\mu_a^{b(K)(1)} - \mu_a^{b(K)(2)} &= \mathbf{E}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)}) - \mathbf{E}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)} | \text{anc}_a(j)) \\
&= \kappa_a^{b(K)},
\end{aligned} \tag{8.19}$$

so that we can write

$$\begin{aligned}
\overline{\phi}_b^{(K)} - \overline{\phi}_a^{(K)} &= S_a^{b(K)} + \mu_a^{b(K)(1)} + M_a^{b(K)(1)} \\
&= S_a^{b(K)} + \mu_a^{b(K)(2)} + M_a^{b(K)(1)} + \mu_a^{b(K)(1)} - \mu_a^{b(K)(2)} \\
&= S_a^{b(K)} + \mu_a^{b(K)(2)} + M_a^{b(K)(1)} + \kappa_a^{b(K)},
\end{aligned} \tag{8.20}$$

which completes the proof. □

Remark 8.14. Note that κ is simply the difference between our previous two transmission and migration terms:

$$\mu_a^{b(K)(1)} = \mu_a^{b(K)(2)} + \kappa_a^{b(K)} \quad (8.21)$$

and

$$M_a^{b(K)(2)} = M_a^{b(K)(1)} + \kappa_a^{b(K)}. \quad (8.22)$$

Note also that if *either* $K(j, b) = K(\text{anc}_a(j))$ for all $j \in R_b$ (meaning that there is no migration) *or* $\phi_j = \phi_{\text{anc}_a(j)}$ (meaning that there is no transmission bias) it follows that $\kappa_a^{b(K)} = 0$. The term $\kappa_a^{b(K)}$ therefore really captures the combined effect of both migration and transmission. It describes how much more likely mutants are to migrate compared to non-mutants, and as such can be seen as a sort of ‘coupling’ term between the two. More specifically, $\kappa_a^{b(K)}$ describes how migration and transmission covary, as I will show later.

We have finally found a version of a local Price Equation that we are satisfied with. I hope I have successfully argued why this equation is best to use. From now on we will refer to the equation in theorem 8.13 as *the* local Price Equation. Also, we will not use the terms $\mu_a^{b(K)(1)}$ and $M_a^{b(K)(2)}$ again, meaning that we can write $\mu_a^{b(K)(2)}$ and $M_a^{b(K)(1)}$ in a simpler way as follows:

Definition 8.15.

$$\mu_a^{b(K)} \equiv \mu_a^{b(K)(2)} \equiv \mathbf{E}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)} | \text{anc}_a(j)) \quad (8.23)$$

and

Definition 8.16.

$$M_a^{b(K)} \equiv M_a^{b(K)(1)} \equiv \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)}) - \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)} | \text{anc}_a(j)). \quad (8.24)$$

Next, we will try to rewrite some of our definitions in covariance terms. We will start with the migration term. Intuitively, one may expect the migration term to be a covariance between phenotype and migration. After all, if replicators with a higher (lower) phenotype tend to immigrate (i.e. get a higher weight), then that would mean a higher covariance between phenotype and immigration, and it would result in a higher (lower) migration term. The covariance between which two terms exactly are we looking for, though? Since the migration term takes no transmission into account, the migration term in between the times a and b should use the phenotype of the replicators living at time a , not at time b . If the migration term is positive, what exactly does this phenotype covary with? That has to be the increase in relative weight, which we can write down as the relative weight at time b of a replicator ($K(j, b) / \sum_{j \in R_b} K(j, b)$) divided by the relative weight of its ancestors ($K(\text{anc}_a(j)) / \sum_{j \in R_b} K(\text{anc}_a(j))$). This leads us to the following claim.

Theorem 8.17. *If $K \neq 0$ for all replicators and all points in time, then*

$$M_a^{b(K)} = \text{Cov}_b^{(K)}(\phi_{\text{anc}_a(j)}, \frac{K(j, b) / \sum_{j \in R_b} K(j, b)}{K(\text{anc}_a(j)) / \sum_{j \in R_b} K(\text{anc}_a(j))} | \text{anc}_a(j)). \quad (8.25)$$

Note that the reason we need to assume weights to be unequal to 0 is because otherwise we would run into divide-by-zero errors. See Appendix C for a proof of theorem 8.17.

Next, we will focus on our term $\kappa_a^{b(K)}$. Earlier we already suspected it to be a covariance between transmission and migration. We can take inspiration from equation 8.25, which describes the covariance between phenotype and migration. To get to the covariance between transmission and migration, we copy equation 8.25 but write down the difference in phenotype between j and its ancestor rather than the phenotype of its ancestor. When we do so, we arrive at the following theorem.

Theorem 8.18. *If $K \neq 0$ for all replicators and all points in time, then*

$$\kappa_a^{b(K)} = \text{Cov}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)}, \frac{K(j, b) / \sum_{j \in R_b} K(j, b)}{K(\text{anc}_a(j)) / \sum_{j \in R_b} K(\text{anc}_a(j))} | \text{anc}_a(j)). \quad (8.26)$$

A proof of this theorem can be found in Appendix C, too.

Remark 8.19. According to a very similar calculation it follows that

$$M_a^{b(K)(2)} = \text{Cov}_b^{(K)}(\phi_j, \frac{K(j, b) / \sum_{j \in R_b} K(j, b)}{K(\text{anc}_a(j)) / \sum_{j \in R_b} K(\text{anc}_a(j))} | \text{anc}_a(j)). \quad (8.27)$$

Other coupling terms

We have introduced $\kappa^{(K)}$ as a sort of coupling term between migration and transmission. This is not the only such term we can define, though. For instance, Okasha [6] has introduced a similar coupling term, but between selection and transmission. This term is obtained by splitting up the transmission term as follows:

$$\begin{aligned}
\mu_a^b &\equiv \mathbf{E}_a(w_a^b \Delta\phi) \\
&= \mathbf{E}_a(\Delta\phi) + \mathbf{E}_a(w_a^b \Delta\phi) - \mathbf{E}_a(\Delta\phi) \\
&= \mathbf{E}_a(\Delta\phi) + \mathbf{E}_a(w_a^b \Delta\phi) - \mathbf{E}_a(\Delta\phi) \mathbf{E}_a(w_a^b) \\
&= \mathbf{E}_a(\Delta\phi) + \text{Cov}_a(w_a^b, \Delta\phi).
\end{aligned} \tag{8.28}$$

Okasha argued that the term $\text{Cov}_a(w_a^b, \Delta\phi)$ should be counted under selection and that $\mathbf{E}_a(\Delta\phi)$ is useful to use as the ‘true’ transmission term. We argue that $\mathbf{E}_a(\Delta\phi)$ could indeed be useful to define as the transmission term. However, we think that instead of seeing $\text{Cov}_a(w_a^b, \Delta\phi)$ as part of selection, one should rather interpret it as a coupling term between selection and transmission.

When extending the Price Equation to a local environment, even more coupling terms like these could be constructed. For example, we could try to find the covariance between selection $S_a^{b(K)}$ and migration, or both the covariance between $\mathbf{E}_a^{(K)}(\Delta\phi)$ and migration, and between $\text{Cov}_a^{(K)}(w_a^b, \Delta\phi)$ and migration. The reason why we have only introduced the term $\kappa^{(K)}$ and not all the other coupling terms is because of the following. We wanted to extend the usual Price Equation to a local Price Equation that incorporates the effect of migration. By doing so, there was ambiguity as to whether the covariance between transmission and migration should fall under the transmission or under the migration term, so for the sake of clarity and to avoid confusion, we introduced this as a term on its own. Although the other coupling terms are interesting and may be useful too, using them did not enhance the clarity in which we could extend the Price Equation to a local environment, which was our only goal in this section.

9 Multilevel selection

Many authors have written on the subject of *multilevel selection*. There are two ways to describe this phenomenon: one is using the *Price Approach* [2] introduced by Price, and the other one is using the *contextual approach* [5] introduced by Heisler and Damuth. In this thesis, we will focus on the Price Approach. To anyone who is interested in an extensive discussion on the differences between the two approaches, as well as a more extensive review of the literature on multilevel selection, I can recommend the master thesis of Laura van Schijndel [7], who also has Rutger Hermsen as a supervisor and who will finish her thesis shortly after I do.

The idea behind the Price Approach of multilevel selection is the following. Suppose that a population of replicators is divided into various different groups. Then we can split the selection term up into two different parts. One part is *intergroup selection* and it describes selection on groups of individuals. The other part is within-group-selection (from now on called *intragroup selection*) and it describes selection on individuals within groups. As an example, suppose that a higher value of ϕ increases the fitness of all of your group members, but slightly decreases one’s own fitness. Then groups with members with high values of ϕ will be successful, so there is intergroup selection for ϕ . Replicators with a high value of ϕ are less fit than replicators with a low value of ϕ that are in the same group, though. As a result, there is intragroup selection against ϕ .

Mathematically we can describe the Price Approach in the following way.

Definition 9.1. Let a *group* be a set of replicators as a function of time. Let g be a group. Then we denote g_t to be the set of replicators that are an element of g at time t . Let \mathcal{G} be a countable set of groups such that for all $t \in I$ and $i \in R_t$, i there is a unique $g \in \mathcal{G}$ such that $i \in g_t$. Note that $(g_t)_{g \in \mathcal{G}}$ forms a partition of R_t if all groups are nonempty at time t .

Definition 9.2. Expected values (or averages) of properties of groups will be taken using the following notation. Let f, h be any real-valued functions of groups. Then if $\sum_{g \in \mathcal{G}} h(g)$ is finite and nonzero, we write

$$\mathbf{E}_{\mathcal{G}}[f|h] \equiv \frac{\sum_{g \in \mathcal{G}} h(g) f(g)}{\sum_{g \in \mathcal{G}} h(g)}. \tag{9.1}$$

This can be interpreted as the expected value of the experiment in which one measures $f(g)$ of a random group g , where the probability to measure g is proportional to $h(g)$. It is easier, though, to think of $\mathbf{E}_{\mathcal{G}}[f|h]$ as the

average of f over all groups, weighted by h . If m is another function that maps a group to a numerical value, the following is the natural extension to our notation of covariance.

$$\text{Cov}_{\mathcal{G}}[f, m|h] \equiv \mathbf{E}_{\mathcal{G}}[fm|h] - \mathbf{E}_{\mathcal{G}}[f|h]\mathbf{E}_{\mathcal{G}}[m|h]. \quad (9.2)$$

Note that we can multiply h with any constant that is unequal to 0 without changing anything to the right hand side of equation 9.1. This is because in this equation, only relative weight matters, and not absolute weight.

We now have notation to take expected values over properties of groups. We will also need notation for expected values of properties of replicators within a group, as opposed to expected values of properties of replicators in the global population.

Definition 9.3. For any function f that maps replicators to numerical values, and for any $g \in \mathcal{G}_t$, we write the following for the expected value of f within group g .

$$\mathbf{E}_t[f|g] \equiv \frac{\sum_{i \in g_t} f(i)}{|g_t|}. \quad (9.3)$$

For m another function that maps replicators to a numerical value, the following is the natural extension to our notation of covariance applied to our new notion of expected value.

$$\text{Cov}_t([f, m|g]) \equiv \mathbf{E}_t(fm|g) - \mathbf{E}_t(f|g)\mathbf{E}_t(m|g). \quad (9.4)$$

Before we can introduce the Price Approach to group selection, we will need the following definition for ease of notation.

Definition 9.4. For all $t \in I$, let $\gamma_t : R_t \rightarrow \mathcal{G}_t$ be the function that maps a replicator to the group it is in, e.g. $\gamma_t(i) = g_t$ where $i \in g_t$ at time t . Let $a, b \in I, a < b$, and let $i \in R_t$. We write the following for the relative fitness of replicator i in its group in the time interval $(a, b]$.

$$w_a^{b(\gamma)}(i) \equiv \frac{W_a^b(i)}{\mathbf{E}_a(W_a^b|\gamma_a(i))}. \quad (9.5)$$

The following two definitions and the following theorem were first introduced by Price [2], though I use my own notation.

Definition 9.5. Let $S_{a,\text{inter}}^b$ be the *intergroup selection term*:

$$S_{a,\text{inter}}^b \equiv \text{Cov}_{\mathcal{G}}[\mathbf{E}_a(\phi|g), \mathbf{E}_a(w_a^b|g)||g_a|]. \quad (9.6)$$

Definition 9.6. Let $S_{a,\text{intra}}^b$ be the *intragroup selection term*:

$$S_{a,\text{intra}}^b \equiv \mathbf{E}_{\mathcal{G}}[\text{Cov}_a(\phi, w_a^{b(\gamma)}|g)||g_b|]. \quad (9.7)$$

Theorem 9.7.

$$S_a^b = S_{a,\text{inter}}^b + S_{a,\text{intra}}^b. \quad (9.8)$$

In 1972, Price proved theorem 9.7 in 1972 [2], albeit using very different notation. Price assumed no migration, though, and theorem 9.7 is not necessarily true if migration is added to the mix. We can, however, make another definition of intragroup selection for which theorem 9.7 is always true, even if we allow migration, and that is equivalent to definition 9.6 if there is no migration. This definition is the following:

Definition 9.8.

$$S_{a,\text{intra}}^b \equiv \mathbf{E}_{\mathcal{G}}[\text{Cov}_a(\phi, w_a^{b(\gamma)}|g_a)||g_a|\mathbf{E}_a(W_a^b|g)]. \quad (9.9)$$

Lemma 9.9. *Definitions 9.6 and 9.8 are equivalent if there is no migration, i.e., if there is no migration, then $S_{a,\text{intra}}^b = S_{a,\text{intra}}^b$.*

Proof. We already know that $N_b = \sum_{i \in R_a} W_a^b(i)$. If there is no migration, one can make a similar statement when restricting the total population to one group. This means that for any $g \in \mathcal{G}$ the following holds.

$$\begin{aligned} |g_b| &= \sum_{i \in g_a} W_a^b(i) \\ &= |g_a|\mathbf{E}_a(W_a^b|g). \end{aligned} \quad (9.10)$$

The lemma follows immediately. □

From now on, we will use definition 9.8 as our definition of intragroup selection. With use of our new definition, we can state a theorem that holds generally, even if we consider migration.

Theorem 9.10.

$$S_a^b = S_{a,\text{inter}}^b + S_{a,\text{intra}}^b. \quad (9.11)$$

We will not yet give a proof of theorem 9.10. Later on, we will extend the notation of multilevel selection to an even more general case, and this is this case for which we will finally give a proof. For now, we will focus on the interpretation of theorem 9.10.

The intergroup selection term is the covariance between average phenotype and average fitness of a group. If this term is positive, then groups with a higher average phenotype tend to have a higher average fitness, and then one could say that there is positive selection for groups with a higher average phenotype. As such, the intergroup selection term describes group selection. The intragroup selection term is the average covariance between phenotype and fitness within each group. If this term is positive, then replicators that have a higher value of ϕ than other members of their group will tend to have a higher fitness than other members of their group. In this case, one could say that there is positive selection for replicators with a higher phenotype than their group members. As such, the intragroup selection term describes selection within groups. Theorem 9.10 describes the intuitive notion that total selection should be the result of both selection within groups and selection among groups.

One might notice that there are certain scenarios in which we would run into trouble by using our definitions. Specifically, if there exists a group that is empty at time a , or in which all replicators die in the time interval $(a, b]$ (meaning the average fitness is zero), the selection term in these groups is undefined, as we run into divide-by-zero errors. As it turns out, this does not need to be a problem at all, though, since we can define selection in such groups in any way we like without making it any difference for the term $S_{a,\text{intra}}^b$ (and since $S_a^b = S_{a,\text{intra}}^b + S_{a,\text{inter}}^b$, neither does it make any difference for the term $S_{a,\text{inter}}^b$). In section 11 we will prove this in a more general case.

10 Extending multilevel selection with the local Price Equation

In section 8 we introduced a weight function $K(i, \tau)$ that describes how much a replicator i ‘counts’ at a time τ . We will now introduce a formalism where we have multiple different weight functions. We will use this new formalism to extend the notion of group selection.

Definition 10.1. Let a weight collection be defined as follows. Let \mathcal{K} be a set of weight functions. Then \mathcal{K} is a weight collection if and only if the following holds for all $t \in I$ and $i \in R_t$.

$$\sum_{K \in \mathcal{K}} K(i, t) = 1. \quad (10.1)$$

From now on, let \mathcal{K} be a weight collection.

Equation 10.1 states that all replicators should have a total weight equal to 1. In the analysis in the upcoming sections, all we really need is for all the replicators to have the same total weight unequal to 0. Since we can always normalize this total weight to 1 without changing anything fundamentally, we can as well make this normalization part of our requirements without loss of generality.

Definition 10.2. Whenever we calculate a property using a weight function $K \in \mathcal{K}$, we denote this by using a superscript (K). We were, of course, already doing so for most terms. We will now extend this notation to all terms, e.g.

$$N_t^{(K)} = \sum_{i \in R_t} K(i, t), \quad (10.2)$$

and we will use different subscripts to denote different weight functions.

Definition 10.3. Let t be any time and K be any weight function. Then we write

$$|K_t| \equiv N_t^{(K)} = \sum_{i \in R_t} K(i, t). \quad (10.3)$$

Definition 10.4. Let $t \in I$ and let f_t, h_t be any real-valued functions of weight functions and R_t . Then we define

$$\mathbf{E}_{\mathcal{K}}(f_t|h_t) \equiv \frac{\sum_{K \in \mathcal{K}} h_t(K, R_t) f_t(K, R_t)}{\sum_{K \in \mathcal{K}} h_t(K, R_t)} \quad (10.4)$$

Suppose that we label our groups $g_1, g_2, \dots \in \mathcal{G}$. For $g_j \in \mathcal{G}$, we denote $g_{j,t}$ as the set of replicator in group g_j at time t , for any $t \in I$. Suppose that we also label our weight functions like this, so we have $K_1, K_2, \dots \in \mathcal{K}$, and $|K_{j,t}| = \sum_{i \in R_t} K_j(i, t)$. Then we can associate every group with a unique weight function as follows:

$$\begin{aligned} K_j(i, t) &= 1 \text{ if } i \in g_{j,t} \\ &= 0 \text{ else .} \end{aligned} \quad (10.5)$$

Since each replicator is in one unique group only, it follows that \mathcal{K} is indeed a weight collection.

In equation 10.5, we are using weight functions to describe groups. One may wonder if we can use these weight functions to describe group selection in an alternative way. This turns out to indeed be the case. We will now prove some intuitive lemmas that will be needed to show this.

Lemma 10.5. *Let the weight functions be as in equation 10.5. Then $|K_{j,t}|$ (from definition 10.3) is equal to $|g_{j,t}|$ (from definition 9.1).*

Proof.

$$|K_{j,t}| \equiv \sum_{i \in R_t} K_j(i, t) = \sum_{i \in g_{j,t}} 1 + \sum_{i \notin g_{j,t}} 0 = \text{Card}(g_{j,t}) \equiv |g_{j,t}|. \quad (10.6)$$

□

Lemma 10.6. *Let the groups and weight functions be as in equation 10.5. Let $(f_\tau)_{\tau \in I}$ be any class of real-valued functions of replicators. Then for all $t \in I$ and all $g_j \in \mathcal{G}$, the following holds.*

$$\mathbf{E}_t(f_t|g_j) = \mathbf{E}_t^{(K_j)}(f_t). \quad (10.7)$$

Proof.

$$\begin{aligned} \mathbf{E}_t(f_t|g_j) &\equiv \frac{\sum_{i \in g_{j,t}} f_t(i)}{|g_{j,t}|} \\ &= \frac{\sum_{i \in R_t} K_j(i, t) f_t(i)}{\sum_{i \in R_t} K_j(i, t)} \\ &\equiv \mathbf{E}_t^{(K_j)}(f_t). \end{aligned} \quad (10.8)$$

□

Lemma 10.7. *Let the groups and weight functions be as in equation 10.5. Let f, h be functions of groups and weight functions such that for all j , $f(g_j) = f(K_j)$ and $h(g_j) = h(K_j)$; i.e. f and h could be interpreted as functions of the indicators used for both groups and weight functions. Then*

$$\mathbf{E}_{\mathcal{G}}(f|h) = \mathbf{E}_{\mathcal{K}}(f|h). \quad (10.9)$$

Proof. Let J be the set of indices of groups and weight functions, so if $g_j \in \mathcal{G}$, then $j \in J$, and vice versa. Then we can write the following.

$$\begin{aligned} \mathbf{E}_{\mathcal{G}}(f|h) &\equiv \frac{\sum_{g_j \in \mathcal{G}} h(g_j) f(g_j)}{\sum_{g_j \in \mathcal{G}} h(g_j)} \\ &= \frac{\sum_{j \in J} h(g_j) f(g_j)}{\sum_{j \in J} h(g_j)} \\ &= \frac{\sum_{j \in J} h(K_j) f(K_j)}{\sum_{j \in J} h(K_j)} \\ &= \frac{\sum_{K_j \in \mathcal{K}} h(K_j) f(K_j)}{\sum_{K_j \in \mathcal{K}} h(K_j)} \\ &\equiv \mathbf{E}_{\mathcal{K}}(f|h). \end{aligned} \quad (10.10)$$

□

Now it is time for our theorems.

Theorem 10.8. *Let our weight functions be as in equation 10.5. Then the following is an alternative expression for intergroup selection.*

$$S_{a,\text{inter}}^b = \text{Cov}_{\mathcal{K}}[\mathbf{E}_a^{(K_j)}(\phi), \mathbf{E}_a^{(K_j)}(w_a^b) | |K_{j,a}|]. \quad (10.11)$$

Proof.

$$\begin{aligned} S_{a,\text{inter}}^b &= \text{Cov}_{\mathcal{G}}[\mathbf{E}_a(\phi | g_j), \mathbf{E}_a(w_a^b | g_j) | |g_{j,a}|] \\ (\text{by lemma 10.6}) &= \text{Cov}_{\mathcal{G}}[\mathbf{E}_a^{(K_j)}(\phi), \mathbf{E}_a^{(K_j)}(w_a^b) | |g_{j,a}|] \\ (\text{by lemma 10.5}) &= \text{Cov}_{\mathcal{G}}[\mathbf{E}_a^{(K_j)}(\phi), \mathbf{E}_a^{(K_j)}(w_a^b) | |K_{j,a}|] \\ (\text{by lemma 10.7}) &= \text{Cov}_{\mathcal{K}}[\mathbf{E}_a^{(K_j)}(\phi), \mathbf{E}_a^{(K_j)}(w_a^b) | |K_{j,a}|]. \end{aligned} \quad (10.12)$$

□

Theorem 10.9. *Let our weight functions be as in equation 10.5. Then the following is an alternative expression for intragroup selection.*

$$S_{a,\text{intra}}^b = \mathbf{E}_{\mathcal{K}}[S_a^{b(K_j)} | |K_{j,a}| \overline{W}_a^{b(K_j)}]. \quad (10.13)$$

Proof.

$$\begin{aligned} S_{a,\text{intra}}^b &= \mathbf{E}_{\mathcal{G}}[\text{Cov}_a(\phi, w_a^{b(\gamma)} | g_{j,a}) | |g_{j,a}| \mathbf{E}_a(W_a^b | g_j)] \\ &= \mathbf{E}_{\mathcal{G}}[\text{Cov}_a(\phi, \frac{W_a^b}{\mathbf{E}_a(W_a^b | \gamma_a)} | g_{j,a}) | |g_{j,a}| \mathbf{E}_a(W_a^b | g_j)] \\ (\text{since } \gamma_a(i) = g_{j,a} \text{ for all } i \in g_{j,a}) &= \mathbf{E}_{\mathcal{G}}[\text{Cov}_a(\phi, \frac{W_a^b}{\mathbf{E}_a(W_a^b | g_{j,a})} | g_{j,a}) | |g_{j,a}| \mathbf{E}_a(W_a^b | g_j)] \\ (\text{by lemma 10.6}) &= \mathbf{E}_{\mathcal{G}}[\text{Cov}_a^{(K_j)}(\phi, \frac{W_a^b}{\mathbf{E}_a^{(K_j)}(W_a^b)} | |g_{j,a}| \mathbf{E}_a^{(K_j)}(W_a^b)] \\ &= \mathbf{E}_{\mathcal{G}}[S_a^{b(K_j)} | |g_{j,a}| \overline{W}_a^{b(K_j)}] \\ (\text{by lemma 10.5}) &= \mathbf{E}_{\mathcal{G}}[S_a^{b(K_j)} | |K_{j,a}| \overline{W}_a^{b(K_j)}] \\ (\text{by lemma 10.7}) &= \mathbf{E}_{\mathcal{K}}[S_a^{b(K_j)} | |K_{j,a}| \overline{W}_a^{b(K_j)}]. \end{aligned} \quad (10.14)$$

□

Corollary 10.10. *The following is also a valid expression for intragroup expression:*

$$\mathbf{E}_{\mathcal{K}}[S_a^{b(K_j)} | \sum_{i \in R_a} K_j(i, a) W_a^b(i)]. \quad (10.15)$$

Proof.

$$\begin{aligned} |K_{j,a}| \overline{W}_a^{b(K)} &= |K_{j,a}| \frac{\sum_{i \in R_a} K_j(i, a) W_a^b(i)}{|K_{j,a}|} \\ &= \sum_{i \in R_a} K_j(i, a) W_a^b(i). \end{aligned} \quad (10.16)$$

The corollary follows from combining this result with theorem 10.9. □

With use of these theorems, we can extend our notions of intra- and intergroup selection in the following way. The following will be our new (and last!) definitions of intergroup and intragroup selection.

Definitions 10.11. Let \mathcal{K} be a weight collection. We denote arbitrary elements of \mathcal{K} as K . Then intergroup selection is defined as follows.

$$S_{a,\text{inter}}^b = \text{Cov}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(\phi), \mathbf{E}_a^{(K)}(w_a^b) | |K_a|]. \quad (10.17)$$

Intragroup selection is defined as follows.

$$S_{a,\text{intra}}^b = \mathbf{E}_{\mathcal{K}}[S_a^{b(K)} | |K_a| \overline{W}_a^{b(K)}]. \quad (10.18)$$

I will argue that definitions 10.11 are a very useful generalization of the idea of multilevel selection. I will mainly focus on intragroup selection in doing so. We have shown that intragroup selection is nothing more than the average of the selection terms in multiple local Price Equations, weighted by the collective fitness of each local group. One reason the generalization is useful is because we can not only perform analysis with the selection term in the local Price Equation, but also with the other terms, or combinations of them. This will be the focus of section 11. Another reason why this generalization is useful is that by using the formalism of weight functions, one can describe multilevel selection in situations where there are no discrete groups to discern. We will give some examples of this.

Example 5. As an example of this last point, suppose that there is some clustering of replicators and that one wants to define groups as clusters. However, some replicators live in between two clusters, making it ambiguous which group they should be assigned to. With our formalism of weight functions, one could associate each cluster with a weight function. The weight function could give a value of 1 to each replicator in the cluster that it is associated with, and a value of $\frac{1}{2}$ to each replicator that is in between the cluster and another cluster.

We can even apply the new definition of intragroup selection *without making any assumption about clustering or groups*.

Example 6. Let $n \in \mathbb{N}$. Suppose that a population of replicators is distributed over a $\mathbb{Z}_n \times \mathbb{Z}_n$ grid. Let x_{it}, y_{it} be the respective x - and y -coordinates of replicator i at time t . Let $m < n$. We define a weight collection \mathcal{K}_m of n^2 different weight functions as follows. For all $0 \leq p, q \leq n$, the following $K_{p,q} \in \mathcal{K}$ exists.

$$K_{p,q}(i, t) = k_{p,q}(x_{it}, y_{it}), \quad (10.19)$$

where

$$k_{p,q}(x, y) = \begin{cases} \frac{1}{m^2} & \text{if } |p - x|, |q - y| \leq m \\ 0 & \text{else} \end{cases} \quad (10.20)$$

We have defined n^2 different weight functions that each correspond to a unique $m \times m$ square on the grid. Every weight functions gives a weight of $\frac{1}{m^2}$ to every replicator in its associated square. Since every replicator is part of m^2 unique $m \times m$ squares, the requirement from equation 10.1 from definition 10.1 is fulfilled. With use of these weight functions, the term $S_{a,\text{intra}}^b$ will only compare relative fitness between replicators that are close to each other on the grid, and hence will describe only how replicators compete with other replicators that are close to them on the grid. The parameter m determines how close on the grid we are looking.

Now it is finally time for the proof of theorem 9.10. It can be found in Appendix D, along with some lemmas that are needed to prove the theorem.

We will end this section with the remark that we could extend the definition of weight collections.

Definition 10.12. We can extend our definitions of weight collections to *uncountable* sets of weight functions. In order to do so, all of the functions in our weight collection must be indexed, and the set of indices must be integrable. Let X be the set of indices. Then equation 10.1 from definition 10.1 can be replaced by the following requirement. For all $t \in I$ and $i \in R_t$, the following equation must hold:

$$\int_X K_x(i, t) dx = 1. \quad (10.21)$$

Any set of weight functions for which this equation holds, will be called a weight collection, too.

As one can verify, all of our results still hold when summations are exchanged for integrals in this way.

11 Global averages of terms in local Price Equations

Previously, we saw that $S_{a,\text{intra}}^b$ equals the average of the local selection terms, weighted by $|K_a|\overline{W}_a^{b(K)}$. I will show more results one can obtain by averaging other local terms using the same weighting. But first we will introduce a new definition in order to make notation easier.

Definition 11.1. Given $a, b \in I, a < b$, a weight collection \mathcal{K} , and P any property of a population of replicators (such as S, μ , etc.), we use the following notation.

$$\widehat{P}_a^b \equiv \mathbf{E}_{\mathcal{K}}[P_a^{b(K)} | |K_a|\overline{W}_a^{b(K)}]. \quad (11.1)$$

We will only use this notation in situations where it is clear what weight collection we are using, since the weight collection \mathcal{K} is missing on the left hand side of the equality.

Remark 11.2. With definition 11.1, our result from theorem 10.9 comes down to

$$S_{a,\text{intra}}^b = \widehat{S}_a^b. \quad (11.2)$$

In this section we will search for more results by calculating \widehat{P} for different properties P . But before doing so, I will tackle some potential problems with the definition of \widehat{P} .

11.1 Making sure our terms are well-defined

The first problem is that all the terms $S_a^{b(K)}, \mu_a^{b(K)}, M_a^{b(K)}, \kappa_a^{b(K)}$ and $\overline{\phi}_a^{(K)}$ are undefined for any weight function K for which $|K_a|\overline{W}_a^{b(K)} = 0$. As such, under the current definitions, the terms $\widehat{S}_a^b, \widehat{\mu}_a^b, \widehat{M}_a^b, \widehat{\kappa}_a^b$ and $\widehat{\phi}_a$ are all undefined if there exists at least one weight function K for which $|K_a|\overline{W}_a^{b(K)} = 0$. We will now tackle this problem with use of the following lemma.

Lemma 11.3. Let \mathcal{K} be a weight collection. Let $h : \mathcal{K} \rightarrow [0, \infty)$ be a nonnegative function of weight functions. let \mathcal{K}_+ be the set of weight functions for which $h(K) > 0$ and let \mathcal{K}_0 be the set of weight functions for which $h(K) = 0$. Let P, P' be any properties of weight functions such that $P \equiv P'$ on all of \mathcal{K}_+ . Then

$$\mathbf{E}_{\mathcal{K}}[P|h(K)] = \mathbf{E}_{\mathcal{K}}[P'|h(K)]. \quad (11.3)$$

Proof. Note that $\mathcal{K} = \mathcal{K}_+ \cup \mathcal{K}_0$. We have

$$\begin{aligned} \mathbf{E}_{\mathcal{K}}[P|h(K)] &= \frac{\sum_{K \in \mathcal{K}} h(K)P(K)}{\sum_{K \in \mathcal{K}} h(K)} \\ &= \frac{\sum_{K \in \mathcal{K}_+} h(K)P(K) + \sum_{K \in \mathcal{K}_0} h(K)P(K)}{\sum_{K \in \mathcal{K}_+} h(K) + \sum_{K \in \mathcal{K}_0} h(K)} \\ &= \frac{\sum_{K \in \mathcal{K}_+} h(K)P(K) + 0}{\sum_{K \in \mathcal{K}_+} h(K) + 0} \\ &= \frac{\sum_{K \in \mathcal{K}_+} h(K)P'(K)}{\sum_{K \in \mathcal{K}_+} h(K)} \\ &= \frac{\sum_{K \in \mathcal{K}_+} h(K)P'(K) + \sum_{K \in \mathcal{K}_0} h(K)P'(K)}{\sum_{K \in \mathcal{K}_+} h(K) + \sum_{K \in \mathcal{K}_0} h(K)} \\ &= \frac{\sum_{K \in \mathcal{K}} h(K)P'(K)}{\sum_{K \in \mathcal{K}} h(K)} \\ &= \mathbf{E}_{\mathcal{K}}[P'|h(K)]. \end{aligned} \quad (11.4)$$

□

This means that the property P only needs to be defined in groups for which $h(K) > 0$, as its definition on groups for which $h(K) = 0$ is irrelevant for the term $\mathbf{E}_{\mathcal{K}}[P|h(K)]$. This means we can use any convention for the definition of a property P on a group K for which $h(K) = 0$.

Definition 11.4. As a convention, whenever a property P is otherwise undefined on a weight function K for which $h(K) = 0$, we will instead write $P^{(K)} \equiv 0$.

With this arbitrary convention, \widehat{S}_a^b , $\widehat{\mu}_a^b$ and $\widehat{\phi}_a$ are all well defined. However, we still run into trouble in the definitions of \widehat{M}_a^b , $\widehat{\kappa}_a^b$ and $\widehat{\phi}_b$, for the terms $M_a^{b(K)}$, $\kappa_a^{b(K)}$ and $\overline{\phi}_b^{(K)}$ all require $|K_b| > 0$, which, because of migration, does not need to be the case even if $|K_a| \overline{W}_a^{b(K)} = 0$. We solve this by introducing the following convention.

Definition 11.5. For every weight functions K for which $|K_b| = 0$, we write $M_a^{b(K)} \equiv \kappa_a^{b(K)} \equiv 0$ and $\overline{\phi}_b^{(K)} \equiv \overline{\phi}_a^{(K)} + S_a^{b(K)} + \mu_a^{b(K)}$.

With these definitions, we still have $\overline{\phi}_b^{(K)} - \overline{\phi}_a^{(K)} = S_a^{b(K)} + \mu_a^{b(K)} + M_a^{b(K)} + \kappa_a^{b(K)}$.

11.2 Calculating the other terms

I will now calculate averages of local terms other than selection. I will start by busting a myth. It is tempting to assume local changes in phenotype to average out to global changes in phenotype. That could be written down in the following formula:

$$\text{(Conjecture)} \quad \widehat{\overline{\phi}_b - \overline{\phi}_a} = \overline{\phi}_b - \overline{\phi}_a. \quad (11.5)$$

However, in general equation 11.5 is false, and it can easily be seen why. Suppose that all transmission is faithful and no migration occurs. Then equation 11.5 would imply the following.

$$\begin{aligned} S_{a,\text{intra}}^b &= \widehat{S}_a^b \\ \text{(since transmission is faithful and there is no migration)} &= \widehat{\overline{\phi}_b - \overline{\phi}_a} \\ \text{(applying the conjecture, equation 11.5)} &= \overline{\phi}_b - \overline{\phi}_a \\ &= S_a^b. \end{aligned} \quad (11.6)$$

This means that $S_{a,\text{inter}}^b$ is always equal to 0 and intergroup selection does not exist, which is clearly not true. I will also introduce an example that illustrates why equation 11.5 is false.

Example 7. Suppose that there are four replicators, called $\alpha, \beta, \gamma, \delta$. The replicators α, β will be in group g_1 at all times, the replicators γ, δ will be in group g_2 at all times, and weight functions are defined as in equation 10.5. Let $\phi_\alpha = 1$, $\phi_\beta = 2$, $\phi_\gamma = 3$ and $\phi_\delta = 4$. Let $W(\alpha) = W(\delta) = 1$, $W(\beta) = 2$ and $W(\gamma) = 0$. Then we can calculate the following:

$$(\overline{\phi}_b - \overline{\phi}_a)^{(K_1)} = \frac{1 + 2 \cdot 2}{3} - \frac{1 + 2}{2} = \frac{5}{3} - \frac{3}{2} = \frac{1}{9} > 0. \quad (11.7)$$

$$(\overline{\phi}_b - \overline{\phi}_a)^{(K_2)} = \frac{4}{1} - \frac{3 + 4}{2} = 4 - \frac{7}{2} = \frac{1}{2} > 0. \quad (11.8)$$

Since both $(\overline{\phi}_b - \overline{\phi}_a)^{(K_1)} > 0$ and $(\overline{\phi}_b - \overline{\phi}_a)^{(K_2)} > 0$, it follows that $\widehat{\overline{\phi}_b - \overline{\phi}_a} > 0$ as well. The following would contradict this if equation 11.5 were true.

$$\overline{\phi}_b - \overline{\phi}_a = \frac{1 + 2 \cdot 2 + 4}{4} - \frac{1 + 2 + 3 + 4}{4} = \frac{9}{4} - \frac{10}{4} = -\frac{1}{4} < 0. \quad (11.9)$$

We can interpret this as follows. The term $\widehat{\overline{\phi}_b - \overline{\phi}_a}$ is positive because in local environments, the average value of ϕ is increasing. But the term $\overline{\phi}_b - \overline{\phi}_a$ is negative because globally, the average value of ϕ is decreasing, and this is due to the local environment with the lowest average value of ϕ having the highest average fitness. There is intergroup selection against ϕ .

Some local terms do average out to their global analogues, though. The following theorem shows that this is the case for transmission.

Theorem 11.6.

$$\widehat{\mu}_a^b = \mu_a^b. \quad (11.10)$$

We will make use of the following lemma to prove this theorem.

Lemma 11.7. For any property P_a^b , the following equality holds.

$$\widehat{P}_a^b = \frac{\sum_{K \in \mathcal{K}} \sum_{i \in R_a} K(i, a) W_a^b(i) P_a^{b(K)}}{N_b}. \quad (11.11)$$

Proof. First note the following.

$$\begin{aligned}
\sum_{K \in \mathcal{K}} \sum_{i \in R_a} K(i, a) W_a^b(i) &= \sum_{i \in R_a} \left(\sum_{K \in \mathcal{K}} K(i, a) \right) W_a^b(i) \\
&= \sum_{i \in R_a} W_a^b(i) \\
&= N_b.
\end{aligned} \tag{11.12}$$

This implies that

$$\begin{aligned}
\widehat{P}_a^b &= \mathbf{E}_{\mathcal{K}}[P_a^{b(K)} | \sum_{i \in R_a} K(i, a) W_a^b(i)] \\
&= \frac{\sum_{K \in \mathcal{K}} \sum_{i \in R_a} K(i, a) W_a^b(i) P_a^{b(K)}}{\sum_{K \in \mathcal{K}} \sum_{i \in R_a} K(i, a) W_a^b(i)} \\
&= \frac{\sum_{K \in \mathcal{K}} \sum_{i \in R_a} K(i, a) W_a^b(i) P_a^{b(K)}}{N_b}.
\end{aligned} \tag{11.13}$$

□

From now on, we will continue to use this lemma without mentioning it.

We are now equipped to prove theorem 11.6. We will directly apply the previous lemma.

Proof.

$$\begin{aligned}
\widehat{\mu}_a^b &= \frac{1}{N_b} \sum_{K \in \mathcal{K}} \sum_{i \in R_a} K(i, a) W_a^b(i) \mu_a^{b(K)} \\
&= \sum_{K \in \mathcal{K}} \sum_{i \in R_a} K(i, a) W_a^b(i) \mathbf{E}_b(\phi_j - \phi_{\text{anc}_a(j)} | \text{anc}_a(j)) \\
&= \frac{1}{N_b} \sum_{K \in \mathcal{K}} \sum_{i \in R_a} K(i, a) W_a^b(i) \frac{\sum_{j \in R_b} K(\text{anc}_a(j)) (\phi_j - \phi_{\text{anc}_a(j)})}{\sum_{j \in R_b} K(\text{anc}_a(j))} \\
&= \frac{1}{N_b} \sum_{K \in \mathcal{K}} \frac{\sum_{i \in R_a} K(i, a) W_a^b(i)}{\sum_{j \in R_b} K(\text{anc}_a(j))} \sum_{j \in R_b} K(\text{anc}_a(j)) (\phi_j - \phi_{\text{anc}_a(j)}) \\
\text{(using lemma 2.10)} &= \frac{1}{N_b} \sum_{K \in \mathcal{K}} \sum_{j \in R_b} K(\text{anc}_a(j)) (\phi_j - \phi_{\text{anc}_a(j)}) \\
&= \frac{1}{N_b} \sum_{j \in R_b} \left(\sum_{K \in \mathcal{K}} K(\text{anc}_a(j)) \right) (\phi_j - \phi_{\text{anc}_a(j)}) \\
&= \frac{1}{N_b} \sum_{j \in R_b} (\phi_j - \phi_{\text{anc}_a(j)}) \\
&\equiv \mu_a^b.
\end{aligned} \tag{11.14}$$

□

Encouraged by the previous result, we might think that something similar ought to be the case for migration. Migration obviously has no effect on the *global* mean phenotype. Should averaging over local migration not be the same as describing global migration? Should we not end up with 0 when we do so, since there are no net migration effects globally? We may think that at least one of the following equations is correct:

$$\begin{aligned}
\text{(Conjecture)} \quad \widehat{M}_a^b &= 0; \\
\text{(Conjecture)} \quad \widehat{\kappa}_a^b &= 0; \\
\text{(Conjecture)} \quad \widehat{M} + \widehat{\kappa}_a^b &= 0.
\end{aligned} \tag{11.15}$$

Alas! They are all only true under special circumstances. In fact, it is not difficult to think of cases in which the migration term does not equal 0.

Example 8. Suppose we have 2 groups, g_1 and g_2 , and weight functions as in equation 10.5. At time a , the average phenotype in group g_1 is ϕ and in g_2 the average phenotype is lower than ϕ . Suppose that nothing happens in between time a and b except for 1 replicator with phenotype ϕ migrating from group g_1 into group g_2 . Its migration will not have any effect on the average phenotype in group g_1 , meaning that $M_a^{b(K_1)} = 0$. However, it will cause the average phenotype in g_2 to increase, meaning that $M_a^{b(K_2)} > 0$. Then the average of the local migration terms will also be strictly positive.

A good question to ask is then: If the migration terms do *not* average out to 0, what do they *mean*? As it turns out, this is a rather hard question. A discussion of the meaning of the averages of the migration terms can be found in Appendix E. Here we will just summarize some findings. The average of the migration terms is the covariance between phenotype and *tendency to end up in environments that other replicators do not end up in*. As a consequence, if for all weight functions $K \in \mathcal{K}$, migration has no effect on the size of K (i.e. $|K_b| = |K_a| \overline{W_a^{b(K)}}$) (this is the case if for instance weight functions are defined as in equation 10.5, and as many replicator migrate into every group as out of every group in the time interval $(a, b]$), then the averages of the migration terms are all equal to 0. A proof can be found in Appendix E.

Remark 11.8. Let us take a step back and use our new definitions of averages of local terms to express the global change in average phenotype. From everything that we have shown so far follows that

$$\begin{aligned}
\overline{\phi_b} - \overline{\phi_a} &= S_a^b + \mu_a^b \\
&= S_{a,\text{inter}}^b + S_{a,\text{intra}}^b + \mu_a^b \\
&= S_{a,\text{inter}}^b + \widehat{S}_a^b + \widehat{\mu}_a^b \\
&= S_{a,\text{inter}}^b + (S_a^b + \mu_a^b + \widehat{M}_a^b + \widehat{\kappa}_a^b) - (\widehat{M}_a^b + \widehat{\kappa}_a^b) \\
&= S_{a,\text{inter}}^b + (\widehat{\phi_b} - \widehat{\phi_a}) - (\widehat{M}_a^b + \widehat{\kappa}_a^b).
\end{aligned} \tag{11.16}$$

Put in words, the global change in average phenotype is the intergroup selection term plus the global average of the local change in average phenotype, minus a correction of an average of migration. All averages are weighted to collective fitness, i.e. how many individual replicators a group leaves as offspring.

12 Combining the local Price Equation with our limit definition of selection

In section 3 up to section 7 we have discussed problems with the intuition behind the term in the Price Equation. We formulated alternative definitions for selection and transmission. We eventually introduced ‘limit’ definitions S_a^b and U_a^b . In section 8, we moved to a different topic: the local Price Equation. Here we introduced the terms $S_a^{b(K)}$, $\mu_a^{b(K)}$, $M_a^{b(K)}$ and $\kappa_a^{b(K)}$. The problems we discussed in section 3 still apply to the terms in the local Price Equation: locally on large time scales, transmission effects and selection effects may get muddled with each other, and maybe with migration effects, too. The same analysis from section 3 up to section 7 can be done for the terms in the local Price Equation, which leads to new definitions. In this section we will explore this approach and introduce terms that combine previous definitions, like $S_a^{b(K)}$.

In the proofs of the theorems in this section we will (finally) make use of the third and fourth requirements from definition 8.1. As such, now seems to be an appropriate time to pause and think about these requirements more.

Remark 12.1. It seems not immediately obvious why we have chosen for the third and fourth requirements from definition 8.1. As we will see soon, these requirements are needed to make sure certain important limits actually exist.

You may have noticed that we have *almost* required our weight functions to be continuous. If our third requirement had been a bit stronger - namely ‘all weight functions are left continuous in time’ - then our third and fourth requirements together would just have been equivalent to ‘all weight functions are continuous in time’. We do not want to assume that, though. One can e.g. imagine replicators making discrete ‘jumps’ in simulations, so requiring continuity would hurt the applicability of our definitions.

You may wonder why we have chosen our weight functions to be right continuous and for left limits to exist instead of the other way around, i.e. for right limits to exist and for weight functions to be left continuous.

The reason is because of the following. Let i be some replicator and let f be a function of time defined as follows.

$$\begin{aligned} f(t) &= 1 \text{ if } i \text{ is alive} \\ &= 0 \text{ else.} \end{aligned} \tag{12.1}$$

As replicators live in time intervals of the form $[a, b)$, this function is right continuous everywhere, but not left continuous at time b (though all of its left limits exist). Since f precisely indicates the domain of $K(i|t)$, it seems appropriate to assume that weight functions are right continuous, rather than left continuous, in time.

The assumption that all weight functions are right continuous is somewhat restrictive. Note though that even if for some replicator, the weight function K is not right continuous, it can be made right continuous by defining a new weight function $K'(t) \equiv K(t)^- = \lim_{\epsilon \downarrow 0} K(t + \epsilon)$, so long as the right limits at least exist.

Recall the following equation from theorem 6.3.

$$S_a^b = \sum_{i=1}^n \frac{\phi_{r_i} - \overline{\phi_{t_i}}}{N_{t_i}} + \sum_{j=1}^m \frac{\overline{\phi_{t_j}} - \phi_{d_j}}{N_{t_j}}. \tag{12.2}$$

We can extend theorem 6.3 to a local environment. But first, we will give one more definition.

Definition 12.2. Let P_a^b be any property of a population of replicators defined on any time interval in the form $(a, b]$ and let t_1, t_2 be any two times. Then we write the following.

$$\begin{aligned} P_{t_1-}^{t_2} &\equiv \lim_{\epsilon \downarrow 0} P_{t_1-\epsilon}^{t_2} \\ P_{t_1}^{t_2-} &\equiv \lim_{\epsilon \downarrow 0} P_{t_1}^{t_2-\epsilon}. \end{aligned} \tag{12.3}$$

This is an extension of definition 6.2.

Theorem 12.3. Let $a < b$. Let r_1, r_2, \dots, r_n be the replication events in the time interval $(a, b]$ and let d_1, d_2, \dots, d_m be the death events in the time interval $(a, b]$. Let t_i, t_j be the respective times of replication event r_i and death event d_j . Let ϕ_{r_i} be the phenotype of the replicator reproducing in replication event r_i , let $K^-(r_i)$ be its weight at time $t_i^- \equiv \lim_{\epsilon \downarrow 0} t_i - \epsilon$ and $K(\text{anc}_s(r_i))$ the weight of its ancestor at time $s \in I$, let ϕ_{d_j} be the phenotype of the replicator dying in replication event d_j , let $K(d_j)$ be its weight at time $t_j^- \equiv \lim_{\epsilon \downarrow 0} t_j - \epsilon$ and let $K(\text{anc}_s(d_j))$ the weight of its ancestor at time $s \in I$. Furthermore, let $\overline{\phi_{t_i}} \equiv \lim_{\epsilon \downarrow 0} \overline{\phi_{t_i-\epsilon}}$. Then the following equality holds.

$$S_a^{b(K)} = \sum_{i=1}^n \frac{K^-(r_i)(\phi_{r_i} - \overline{\phi_{t_i}})}{|K_{t_i}^-| W_{t_i-}^{t_i}} + \sum_{j=1}^m \frac{K^-(d_j)(\overline{\phi_{t_j}} - \phi_{d_j})}{|K_{t_j}^-| W_{t_i-}^{t_i}}. \tag{12.4}$$

We require $|K_{t_i}^-| W_{t_i-}^{t_i}, |K_{t_j}^-| W_{t_i-}^{t_i} \neq 0$ for all t_i, t_j .

A proof of theorem 12.3, as well as a proof of the following corollary, can be found in Appendix F.

Corollary 12.4. Let U be the set of times in the time interval $(a, b]$ that replication or death occurs. For $t_j \in U$, let n_j, m_j be the respective number of replication and death events at time t_j and let $(r_{j,i}, 0 \leq i \leq n_j), (d_{j,i}, 0 \leq i \leq m_j)$ be the respective replication and death events at time t_j . Then

$$\begin{aligned} &S_a^{b(K)} \\ &= \sum_{t_j \in U} \left(\sum_{i=1}^{n_j} \frac{K^-(r_{j,i})(\phi_{r_{j,i}} - \overline{\phi_{t_j}})}{|K_{t_j}^-| + \sum_{i'=1}^{n_j} K^-(r_{j,i'}) - \sum_{i'=1}^{m_j} K^-(d_{j,i'})} + \sum_{i=1}^{m_j} \frac{K^-(d_{j,i})(\overline{\phi_{t_j}} - \phi_{d_{j,i}})}{|K_{t_j}^-| + \sum_{i'=1}^{n_j} K^-(r_{j,i'}) - \sum_{i'=1}^{m_j} K^-(d_{j,i'})} \right). \end{aligned} \tag{12.5}$$

Remark 12.5. The existence of left limits in time of weight functions to exist is really a necessary requirement, as can be demonstrated with a simple example. Suppose that a replicator i lives in the time interval $[0, 1)$ and its weight function is described by $K(i|t) = \frac{1}{2} \sin(1/(1-t)) + \frac{1}{2}$. Since the function $\sin(1/(1-t))$ behaves highly erratic around $t = 1$, we cannot really say what its weight function looks like at the ‘moment of its death’, and hence cannot say how much the death ‘counts’. In this case S_a^b does not converge.

Recall from theorem 7.7 that if we define the phenotype of the replicator being born in replication event r_i minus that of its parent as $\Delta\phi_{r_i}$, we have the following expression.

$$\mathcal{U}_a^b = \sum_{i=1}^n \frac{\Delta\phi_{r_i}}{N_{t_i}}. \quad (12.6)$$

Theorem 12.6. *The following expression holds.*

$$\mathcal{U}_a^{b(K)} = \sum_{i=1}^n \frac{K^-(r_i)\Delta\phi_{r_i}}{|K_{t_i}^-|\overline{W}_{t_i-}^{t_i}}. \quad (12.7)$$

We require $|K_{t_i}^-|\overline{W}_{t_i-}^{t_i} \neq 0$ for all $1 \leq i \leq n$.

All the steps needed to prove this theorem are analogues to steps taken in the proof of theorem 12.3.

The weight versions of the migration terms of the limit definition of selection are more difficult to obtain. This is because of two problems. The first problem is that while we used the proof of the expression for the limit definition of global selection, \mathcal{S}_a^b , as a starting point for the proof of theorem 12.3, there is no analogue to this with regards to migration. The reason is that there is no such thing as a global migration term. As such, finding weight versions of the migration terms of the limit definition of selection is not analogous to anything we have done before. We can work with our non-limit weight definition of migration as a starting point, though. As a reminder, these are given by the following equations.

$$\begin{aligned} M_a^{b(K)} &\equiv \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)}) - \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)}|\text{anc}_a(j)) \\ \kappa_a^{b(K)} &\equiv \mathbf{E}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)}) - \mathbf{E}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)}|\text{anc}_a(j)). \end{aligned} \quad (12.8)$$

The following definitions come naturally.

Definitions 12.7. Let $k \in \mathbb{N}$. We define $j \equiv \frac{b-a}{k}$.

$$\begin{aligned} M_a^{b,k(K)} &\equiv \sum_{s=0}^{k-1} M_{a+sj}^{a+(s+1)j}, \\ \kappa_a^{b,k(K)} &\equiv \sum_{s=0}^{k-1} \kappa_{a+sj}^{a+(s+1)j}. \end{aligned} \quad (12.9)$$

Definitions 12.8.

$$\begin{aligned} \mathcal{M}_a^{b,k(K)} &\equiv \lim_{k \uparrow \infty} M_a^{b,k}; \\ \mathcal{K}_a^{b,k(K)} &\equiv \lim_{k \uparrow \infty} \kappa_a^{b,k}. \end{aligned} \quad (12.10)$$

One may think that it is not very complicated to just fill in expressions 12.8 into definitions 12.7 and then take the limit. The second problem we encounter, however, is that while the transmission and selection terms are only influenced by what happens in a strict number of discrete events, this is not necessarily the case for migration. This makes using sums cumbersome. Luckily, as it turns out we can show that we can take the limit of the sums and that the limit exists. We have to use the fact that weight functions are right continuous in time in order to do so. This can be used to prove the following.

Theorem 12.9. *Let $a < b$ and let K be a weight function. Let $|K_t| \neq 0$ for all $t \in (a, b]$. Let U be the set of times that a replication and/or death event occurs in the time interval $(a, b]$, with $U \equiv \{t_1, t_2, \dots, t_{|U|}\}$. Then the following two equations hold.*

$$\mathcal{M}_a^{b,k(K)} = M_a^{t_1-(K)} + M_{t_1}^{t_2-(K)} + \dots + M_{t_{|U|}}^{b-(K)} + \sum_{t_j \in U} M_{t_j-}^{t_j-(K)}; \quad (12.11)$$

$$\mathcal{K}_a^{b,k(K)} = \sum_{t_j \in U} \kappa_{t_j-}^{t_j-(K)}. \quad (12.12)$$

A proof of this theorem, as well as a lemma needed for the proof, can be found in Appendix G.

Corollary 12.10. *If weight functions are continuous in time and children have the same weight as their parents at the time of birth (i.e. $K^-(i, t) = K(j, t)$ if j is born at time t from parent i), then the following equations hold.*

$$\mathcal{M}_a^{b,k(K)} = M_a^{t_1^-(K)} + M_{t_1^-}^{t_2^-(K)} + \dots + M_{t_{|U|}^-}^b(K); \quad (12.13)$$

$$\mathcal{K}_a^{b,k(K)} = 0. \quad (12.14)$$

Proof. Under the assumptions of the corollary, it follows that

$$\sum_{t_j \in U} M_{t_j^-}^{t_j^-(K)} = \sum_{t_j \in U} \kappa_{t_j^-}^{t_j^-(K)} = 0. \quad (12.15)$$

Then the corollary follows immediately from theorem 12.9. \square

We now have all the limit definitions of the local Price Equation.

13 Global averages of limit terms in local Price Equations

In the previous section, we found ‘limit’ versions of terms in the local Price Equation: $S_a^{b(K)}$, $U_a^{b(K)}$, $\mathcal{M}_a^{b(K)}$ and $\mathcal{K}_a^{b(K)}$. In sections 10 and 11 we introduced *weight collections* to average local terms over a global environment. In this section, we will combine work from all previous sections to use weight collections to average the limit terms of the local Price Equation over a global environment. This will lead to expressions for global averages of local selection, transmission, and migration, measured on infinitesimal time scales.

13.1 Explaining the definitions

Definition 13.1. Let P_a^b be any property defined on any time interval in the form $(a, b]$ (e.g. $P_a^b = S_a^b$ or $P_a^b = \mu_a^b$ or $P_a^b = M_a^b$ or $P_a^b = \kappa_a^b$). For any such property, we define, per the usual notation, the following for all $k \in \mathbb{N}$ and $j \equiv \frac{b-a}{k}$.

$$\widehat{P}_a^{b,k} \equiv \widehat{\left(\sum_{s=0}^{k-1} P_{a+sj}^{a+(s+1)j} \right)} = \sum_{s=0}^{k-1} \widehat{P}_{a+sj}^{a+(s+1)j}. \quad (13.1)$$

Remark 13.2. According to our definition of $\widehat{P}_a^{b,k}$, we can write

$$\widehat{P}_a^{b,k} = \sum_{s=0}^{k-1} \mathbf{E}_{\mathcal{K}} [P_{a+sj}^{a+(s+1)j} | |K_{a+sj}| \overline{W_{a+sj}^{a+(s+1)j}}^{(K)}]. \quad (13.2)$$

There seems to be another way in which definitions could be extended to global averages. We may be tempted to think that we could also define

$$\widehat{P}_a^{b,k} = \mathbf{E}_{\mathcal{K}} \left[\sum_{s=0}^{k-1} P_{a+sj}^{a+(s+1)j} | |K_{a+sj}| \overline{W_{a+sj}^{a+(s+1)j}}^{(K)} \right], \quad (13.3)$$

but then we would be mistaken, as this expression is not properly defined. This is because the previous expression can be written as follows.

$$\mathbf{E}_{\mathcal{K}} \left[\sum_{s=0}^{k-1} P_{a+sj}^{a+(s+1)j} | |K_{a+sj}| \overline{W_{a+sj}^{a+(s+1)j}}^{(K)} \right] = \frac{\sum_{K \in \mathcal{K}} |K_{a+sj}| \overline{W_{a+sj}^{a+(s+1)j}}^{(K)} \sum_{s=0}^{k-1} \sum_{K \in \mathcal{K}} P_{a+sj}^{a+(s+1)j}(K)}{|K_{a+sj}| \overline{W_{a+sj}^{a+(s+1)j}}^{(K)}}. \quad (13.4)$$

Here, there are a lot of terms containing the variable s outside of the environment where we sum over s , and hence the expression makes no sense. Intuitively, this can be understood as follows. With the approach in equation 13.3 we sum over time intervals before we assign weight to groups. But we have to assign weights first, because group weight can change over time. Clearly, the expression in equation 13.3 is nonsensical, and the expression in equation 13.2 is the right one.

The following lemma will be useful in order to prove the upcoming theorems.

Lemma 13.3. *Given k , let τ_s be defined as in definition G.2. The following expression holds.*

$$\lim_{k \uparrow \infty} \widehat{P}_a^{b,k} = \lim_{k \uparrow \infty} \sum_{s=0}^{k-1} \widehat{P}_{\tau_s}^{\tau_{s+1}}. \quad (13.5)$$

Proof. The lemma follows from applying the definitions.

$$\begin{aligned} \lim_{k \uparrow \infty} \widehat{P}_a^{b,k} &= \lim_{k \uparrow \infty} \left(\sum_{s=0}^{k-1} \widehat{P}_{a+s(b-a)/k}^{a+(s+1)(b-a)/k} \right) \\ &= \lim_{k \uparrow \infty} \left(\sum_{s=0}^{k-1} \widehat{P}_{\tau_s}^{\tau_{s+1}} \right) \\ &= \lim_{k \uparrow \infty} \sum_{s=0}^{k-1} \widehat{P}_{\tau_s}^{\tau_{s+1}}. \end{aligned} \quad (13.6)$$

□

13.2 Selection

We define, per the usual notation, the following.

Definitions 13.4. Let $a, b \in I$, $a < b$, and $k \in \mathbb{N}$. We write $j \equiv \frac{b-a}{k}$.

$$\begin{aligned} S_{a,\text{inter}}^{b,k} &\equiv \sum_{s=0}^{k-1} S_{a+s j, \text{inter}}^{a+(s+1)j}, \\ S_{a,\text{intra}}^{b,k} &\equiv \sum_{s=0}^{k-1} S_{a+s j, \text{intra}}^{a+(s+1)j}. \end{aligned} \quad (13.7)$$

Definition 13.5.

$$\widehat{S}_a^b \equiv \lim_{k \uparrow \infty} \widehat{S}_a^{b,k}. \quad (13.8)$$

Note that thanks to definition 9.8 we know that for all times $x, y, x < y$ we have

$$S_{x,\text{intra}}^y = \widehat{S}_x^y, \quad (13.9)$$

so that

$$\begin{aligned} \widehat{S}_a^b &= \lim_{k \uparrow \infty} \left(\sum_{s=0}^{k-1} \widehat{S}_{\tau_s}^{\tau_{s+1}} \right) \\ &= \lim_{k \uparrow \infty} \sum_{s=0}^{k-1} S_{\tau_s, \text{intra}}^{\tau_{s+1}} \\ &= \lim_{k \uparrow \infty} S_{a,\text{intra}}^{b,k}, \end{aligned} \quad (13.10)$$

so finding the limit version of intragroup selection is the same as finding the global average of local selection terms. The following theorem gives an expression for this in terms of individual births and deaths. Note the similarities with theorem 6.3.

Theorem 13.6. *Let $a < b$. Let r_1, r_2, \dots, r_n be the replication events and let d_1, d_2, \dots, d_m be the death events in the time interval $(a, b]$. Let t_i, t_j be the respective times of replication event t_i and death event d_j . Let r_i and d_j be the respective replicator that replicates in replication event r_i and that dies in death event d_j . Then*

$$\widehat{S}_a^b = \sum_{i=1}^n \frac{\phi_{r_i} - \mathbf{E}_{\mathcal{K}}[\phi_{t_i}^- | K^-(r_i, t_i)]}{N_{t_i}} + \sum_{j=1}^m \frac{\mathbf{E}_{\mathcal{K}}[\phi_{t_j}^- | K^-(d_j, t_j)] - \phi_{d_j}}{N_{t_j}}. \quad (13.11)$$

A proof of theorem 13.6 can be found in Appendix H. In this appendix an analogue to lemma 4.2 can be found, too.

Corollary 13.7.

$$S_{a,\text{inter}}^{b,k} = \sum_{i=1}^n \frac{\mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_j}^{(K)}} | K(r_i)] - \overline{\phi_{t_i}}}{N_{t_i}} + \sum_{K \in \mathcal{K}} \frac{\overline{\phi_{t_j}} - \mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_j}^{(K)}} | K(d_j)]}{N_{t_j}}. \quad (13.12)$$

Proof. Since for all $x, y, x < y$ we have

$$\begin{aligned} S_x^y &= S_{x,\text{inter}}^y + S_{x,\text{intra}}^y = S_{x,\text{inter}}^y + \widehat{S}_x^y \\ \implies S_{x,\text{inter}}^y &= S_x^y - \widehat{S}_x^y, \end{aligned} \quad (13.13)$$

from which the following follows.

$$\begin{aligned} S_{a,\text{inter}}^{b,k} &= \lim_{k \uparrow \infty} S_a^{k,(b-a)/k} - \widehat{S}_a^b \\ &= \sum_{i=1}^n \frac{\phi_{r_i} - \overline{\phi_{t_i}}}{N_{t_i}} + \sum_{K \in \mathcal{K}} \frac{\overline{\phi_{t_j}} - \phi_{d_j}}{N_{t_j}} \\ &\quad - \left(\sum_{i=1}^n \frac{\phi_{r_i} - \mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_i}^{(K)}} | K(r_i)]}{N_{t_i}} + \sum_{j'=1}^m \frac{\mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_j}^{(K)}} | K(d_j)] - \phi_{d_j}}{N_{t_j}} \right) \\ &= \sum_{i=1}^n \frac{\mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_j}^{(K)}} | K(r_i)] - \overline{\phi_{t_i}}}{N_{t_i}} + \sum_{K \in \mathcal{K}} \frac{\overline{\phi_{t_j}} - \mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_j}^{(K)}} | K(d_j)]}{N_{t_j}}. \end{aligned} \quad (13.14)$$

□

13.3 Transmission

We start with the expected definition:

Definition 13.8.

$$\widehat{\mathcal{U}}_a^b \equiv \lim_{k \uparrow \infty} \widehat{\mu}_a^{b,k}. \quad (13.15)$$

Finding an expression for this is a lot more straightforward than doing so for selection.

Theorem 13.9.

$$\widehat{\mathcal{U}}_a^b = \mathcal{U}_a^b. \quad (13.16)$$

Proof. Theorem 11.6 says that for all $x, y, x < y$ we have

$$\mu_x^y = \widehat{\mu}_x^y, \quad (13.17)$$

and hence

$$\widehat{\mathcal{U}}_a^b = \lim_{k \uparrow \infty} \sum_{s=0}^{k-1} \widehat{\mu}_{\tau_s}^{\tau_{s+1}} = \lim_{k \uparrow \infty} \sum_{s=0}^{k-1} \mu_{\tau_s}^{\tau_{s+1}} = \mathcal{U}_a^b. \quad (13.18)$$

□

13.4 Migration

We will use the following definitions:

Definitions 13.10.

$$\widehat{\mathcal{M}}_a^b \equiv \lim_{k \uparrow \infty} \widehat{M}_a^{b,k}; \widehat{\mathcal{K}}_a^b \equiv \lim_{k \uparrow \infty} \widehat{K}_a^{b,k}. \quad (13.19)$$

In the proof of theorem 12.9 we used lemma G.1 to show that in the calculation of $\mathcal{M}_a^{b,k}$ and $\mathcal{K}_a^{b,k}$, we could throw away all values of the weight functions in between birth and replication events; all that mattered was the values of the weight functions just before and during replication and death events. This was useful, as there are only finitely many such events. Unfortunately, there is no analogue to this for $\widehat{M}_a^{b,k}$. We will show this with an example that is inspired by example 10 on page 47.

Example 9. Suppose weight functions are defined as in equation 10.5 and there are only 2 groups with corresponding weight functions, K_1 and K_2 . Suppose that there are 3 replicators, called b_1 , b_2 and b_3 . We have $\phi_{b_1} = \phi_{b_2} = 0$ and $\phi_{b_3} = 1$. Also, $K_{g_1}(b_1|t) \equiv K_{g_2}(b_2|t) \equiv 1$, i.e. b_1 is always in group 1 and b_2 is always in group 2. The only events in the time interval $(a, b]$ are the following: At time t_1 , replicator b_3 moves from group 1 to group 2, and at time $t_2 > t_1$, it moves back to group 1. As you can see, none of the replicators at time b are in a different group than they were at time a , and as such,

$$\widehat{M}_a^b = 0. \quad (13.20)$$

However,

$$\widehat{\mathcal{M}}_a^b = \frac{2}{3} \neq 0 = \widehat{M}_a^b, \quad (13.21)$$

as is shown in Appendix I.1.

Now it is not difficult to see that if replicator b_3 migrates back-and-forth n times, then

$$\widehat{\mathcal{M}}_a^b = \frac{2n}{3}. \quad (13.22)$$

As such, even though no replication or death events are happening, the individual migration events happening in between time a and b are still all relevant for the term $\widehat{\mathcal{M}}_a^b$, and they cannot be reduced to something simpler.

Luckily, there *is* an analogue to lemma G.1 and theorem 12.9 for $\widehat{\kappa}_a^{b,k}$.

Theorem 13.11. *Let $a < b$. Let U be the set of times that a birth and/or death occurs in the time interval $(a, b]$, with $U \equiv \{t_1, t_2, \dots, t_{|U|}\}$. Then*

$$\widehat{\mathcal{U}}_a^b = \sum_{t_{j'} \in U} \widehat{\kappa}_{t_{j'}}^{t_{j'}}. \quad (13.23)$$

See section I.2 for a proof of this theorem.

Corollary 13.12. *If all weight functions are continuous and children have the same weights as their parents (i.e. if i gives birth to j at time t , then for all $K \in \mathcal{K}$, $K(i, t)^- = K(j, t)$), then*

$$\widehat{\mathcal{U}}_a^b = 0. \quad (13.24)$$

Proof. This follows immediately from theorem 12.9. □

14 Conclusion and discussion

We have introduced a definition to study the effect of selection on different scales in time, $S_a^{b,k}$. We also introduced a definition that looks at selection on infinitesimal time scales, \mathcal{S}_a^b . We did the same for transmission. We have also introduced a local Price Equation with which one can study the effects of selection, transmission and migration in local environments. We have also shown a way to average these terms over different local environments. We found that averaging over local selection gives nothing less than an extension to intragroup selection as introduced by Price [2], and we found additional terms for the average of local transmission and migration. We have also combined our approaches to find local expressions for selection, transmission and migration on infinitesimal time scales, and global averages of these expressions.

The focus of this thesis was on mathematics. As such, we spent a lot of time deriving mathematical properties of our various expressions, and not much time on applications. Let me now turn to the examples from the Introduction and show how the definitions introduced by me can be used to make quantifiable statements about intensively studied topics.

Consider the paper of Levin and Bull [3] that was discussed in the Introduction. Levin and Bull argue that a mutation that makes a pathogen more virulent will benefit that pathogen to spread through its current host, but may be a hindrance for the pathogen in the effort of infecting additional hosts, and as such, a mutation to make a pathogen more virulent would only be beneficial ‘locally’, within a host. Suppose we define a collection of weight functions \mathcal{K} . For every host there is a unique $K \in \mathcal{K}$ that assigns a value of 1 to all pathogens within the host, and a value of 0 to all other pathogens. Using the weight collection \mathcal{K} , the term \widehat{S}_a^b would precisely describe within-host selection. If it indicates positive selection for virulence, but S_a^b does not, then that would support the hypothesis of Levin and Bull. Interestingly, the term \widehat{M}_a^b would describe migration between hosts, which in this case comes down to infection. If it is true that virulent pathogens are destined to die out eventually due to not being able to infect additional hosts, then if $b \gg a$, the term S_a^b would indicate selection against virulence, though the term \mathcal{S}_a^b may not, due to virulent pathogens having an initial advantage. That would indicate that being virulent is indeed a short-sighted strategy.

Next, consider the spatial Cooperator-Defector model of Nowak and May [4]. Suppose \mathcal{K} is a weight collection containing weight functions that each give high weight to some group of replicators close together. If Defectors are indeed locally fitter than Cooperators, but not globally, then this would imply that \widehat{S}_a^b indicates selection for Defection, but S_a^b does not. The precise form of \mathcal{K} may quantify exactly *how* local we have to look for Defectors to be fitter than Cooperators. For example, suppose we cover the field with disks of a fixed radius, and every $K \in \mathcal{K}$ gives a positive value to replicators only in a certain disk that is unique for this K . Then by decreasing the radii of the disks, the term \widehat{S}_a^b will look at selection on an increasingly local scale. Also, if Defectors are always destined to leave no offspring on long time scales due to eventually being surrounded by other Defectors, then if $b \gg a$, the term S_a^b would indicate selection for Cooperation; but \mathcal{S}_a^b may not (and in fact, with faithful transmission and in stochastic equilibrium, it must equal *zero* for the Price Equation to hold). This would indicate that Defection really is a short-term strategy. Remember that $S = S_a^{b,1}$ and $\mathcal{S}_a^b = \lim_{k \uparrow \infty} S_a^{b,k}$. The intermediate terms $S_a^{b,k}$ for $1 < k < \infty$ may give a clue to *how* short this ‘short-term strategy’ really is.

The above are mere illustrations of how the definitions introduced in this thesis could be used to make precise statements about selection, and other factors that influence evolution, on multiple scales in both space and time. I hope that I have made a useful addition to the toolbox of theoretical biologists. My hope is that others will deem my definitions helpful and will apply them to their own research. I would be mightily interested in such research and what conclusions would be drawn from them.

Appendix

A Proof of theorem 6.3

Proof. Let U be the set of times that a birth and/or death occurs in the time interval $(a, b]$. If multiple birth and/or death events happen at the same time, they only account for 1 element of U , since a set cannot contain the same element more than once. Let

$$\epsilon^* \equiv \frac{1}{2} \min\{|t - s|, t, s \in U \cup \{a, b\}, t \neq s\} \quad (\text{A.1})$$

Let $t_j \in U$. Let $0 < \epsilon < \epsilon^*$ and $0 \leq \delta < \epsilon^*$. If $t_j = b$, choose $\delta = 0$ instead. Because of our choice of ϵ and δ , the time interval $(t_j - \epsilon, t_j + \delta]$ is a subset of $(a, b]$ (because $t_j - a > \epsilon^* > \epsilon$ and $t_j - b \geq \delta$), and all birth and death events in the time interval $(t_j - \epsilon, t_j + \delta]$ happen at time t_j (because $\epsilon, \delta < \epsilon^*$). Let $r_{j,1}, r_{j,2}, \dots, r_{j,n_j}$ be the replication events at time t_j and let $d_{j,1}, d_{j,2}, \dots, d_{j,m_j}$ be the death events at this time, with n_j the number of birth events at time t_j and m_j the number of death events at time t_j . Then according to lemma 4.2, the following holds.

$$S_{t_j - \epsilon}^{t_j + \delta} = \frac{1}{N_{t_j + \delta}} \left(\sum_{i=1}^{n_j} \phi_{\text{anc}_{t_j - \epsilon}(r_{j,i})} - \sum_{i=1}^{m_j} \phi_{\text{anc}_{t_j - \epsilon}(d_{j,i})} + (N_{t_j - \epsilon} - N_{t_j + \delta}) \overline{\phi_{t_j - \epsilon}} \right) \quad (\text{A.2})$$

Of course, because no replication or death events happen in the time interval $(t_j - \epsilon, t_j)$, and because we assume that no replicator can be born and give birth at the exact same moment in time, every replicator reproducing or dying at time t_j must have the same phenotype as its ancestor at time $t_j - \epsilon$ (because it is its own ancestor). Let $\phi_{r_{j,1}}, \phi_{r_{j,2}}, \dots$ be the phenotypes of the replicators giving birth in the birth events at time t_j and let $\phi_{d_{j,1}}, \phi_{d_{j,2}}, \dots$ be the phenotypes of the replicators that die at time t_j . We can use this to rewrite equation A.2 as follows.

$$\begin{aligned} S_{t_j - \epsilon}^{t_j + \delta} &= \frac{1}{N_{t_j + \delta}} \left(\sum_{i=1}^{n_j} \phi_{r_{j,i}} - \sum_{i=1}^{m_j} \phi_{d_{j,i}} + (N_{t_j - \epsilon} - N_{t_j + \delta}) \overline{\phi_{t_j - \epsilon}} \right) \\ (\text{because } N_{t_j + \delta} &= N_{t_j - \epsilon} + n_j - m_j) &= \frac{1}{N_{t_j + \delta}} \left(\sum_{i=1}^{n_j} \phi_{r_{j,i}} - \sum_{i=1}^{m_j} \phi_{d_{j,i}} + (N_{t_j - \epsilon} - (N_{t_j - \epsilon} + n_j - m_j)) \overline{\phi_{t_j - \epsilon}} \right) \\ &= \frac{1}{N_{t_j + \delta}} \left(\sum_{i=1}^{n_j} \phi_{r_{j,i}} - \sum_{i=1}^{m_j} \phi_{d_{j,i}} + (m_j - n_j) \overline{\phi_{t_j - \epsilon}} \right) \\ &= \frac{1}{N_{t_j + \delta}} \left(\sum_{i=1}^{n_j} (\phi_{r_{j,i}} - \overline{\phi_{t_j - \epsilon}}) + \sum_{i=1}^{m_j} (\overline{\phi_{t_j - \epsilon}} - \phi_{d_{j,i}}) \right) \end{aligned} \quad (\text{A.3})$$

Remember that there are no birth or death events in the time interval $(t_j, t_j + \delta)$ (so $N_{t_j + \delta} = N_{t_j}$) and neither are there birth or death events in the time interval $(t_j - \epsilon, t_j)$ (so $\overline{\phi_{t_j - \epsilon}} = \overline{\phi_{t_j - \epsilon'}}$ for all $0 < \epsilon' < \epsilon$), meaning that $\overline{\phi_{t_j - \epsilon}} = \lim_{\epsilon' \downarrow 0} \overline{\phi_{t_j - \epsilon'}}$. Remember the following:

$$\overline{\phi_t^-} \equiv \lim_{\epsilon \downarrow 0} \overline{\phi_{t - \epsilon}} \quad (\text{A.4})$$

We will use this shorthand notation to rewrite equation A.3 as follows.

$$\begin{aligned} S_{t_j - \epsilon}^{t_j + \delta} &= \frac{1}{N_{t_j}} \left(\sum_{i=1}^{n_j} (\phi_{r_{j,i}} - \overline{\phi_{t_j}^-}) + \sum_{i=1}^{m_j} (\overline{\phi_{t_j}^-} - \phi_{d_{j,i}}) \right) \\ &= \sum_{i=1}^{n_j} \frac{\phi_{r_{j,i}} - \overline{\phi_{t_j}^-}}{N_{t_j}} + \sum_{i=1}^{m_j} \frac{\overline{\phi_{t_j}^-} - \phi_{d_{j,i}}}{N_{t_j}} \end{aligned} \quad (\text{A.5})$$

Let $k > \frac{b-a}{\epsilon^*}$. Then all the selection terms in the summation of $S_a^{b,k}$ that are over a period of time that does not contain an element of U are equal to 0, since these periods of time contain no single birth or death event. Also, all of the selection terms that do contain an element of U , contain only 1 such element because if $k > \frac{b-a}{\epsilon^*}$, the lengths of the time intervals are smaller than $2\epsilon^*$. As such, for all $0 < \epsilon_j < \epsilon^*$ and $0 \leq \delta_j < \epsilon^*$ for all $j \in U$, the following equation holds.

$$\begin{aligned}
S_a^{b,k} &= \sum_{s=0}^{k-1} S_{a+s(b-a)/k}^{a+(s+1)(b-a)/k} \\
&= \sum_{t_j \in U} S_{t_j - \epsilon_j}^{t_j + \delta_j}
\end{aligned} \tag{A.6}$$

Also, for $t_j = b \in U$, we have $\delta_j = 0$ since the last term in the summation must have b as superscript. We have written out these terms in equation A.5, with which we get to the following expression.

$$S_a^{b,k} = \sum_{t_j \in U} \left(\sum_{i=1}^{n_j} \frac{\phi_{r_{j,i}} - \bar{\phi}_{t_j}}{N_{t_j}} + \sum_{i=1}^{m_j} \frac{\bar{\phi}_{t_j} - \phi_{d_{j,i}}}{N_{t_j}} \right) \tag{A.7}$$

Let n be the number of replication events and m the number of death events in the time interval $(a, b]$. Let ϕ_{r_i} be the phenotype of the replicator reproducing in birth event i and let t_i be the time of birth event i . Similarly, let ϕ_{d_j} be the phenotype of the replicator dying in death event j and let t_j be the time of death event j . We can now rewrite equation A.7 into the following.

$$S_a^{b,k} = \sum_{i=1}^n \frac{\phi_{r_i} - \bar{\phi}_{t_i}}{N_{t_i}} + \sum_{j=1}^m \frac{\bar{\phi}_{t_j} - \phi_{d_j}}{N_{t_j}} \tag{A.8}$$

Since this result holds for all $k > \frac{b-a}{\epsilon^*}$, and $\frac{b-a}{\epsilon^*} < \infty$, the same holds for the following limit.

$$S_a^b = \sum_{i=1}^n \frac{\phi_{r_i} - \bar{\phi}_{t_i}}{N_{t_i}} + \sum_{j=1}^m \frac{\bar{\phi}_{t_j} - \phi_{d_j}}{N_{t_j}} \tag{A.9}$$

□

B Proof of theorem 7.7 (shortened)

Because the proof is very analogous to the proof of theorem 6.3, we will not go into too much detail for the proof of theorem 7.7.

Proof. (of theorem 7.7) Let $U, \epsilon^*, t_j, \epsilon, \delta$ as in the proof of theorem 6.3. Let $r_{j,1}, r_{j,2}, \dots, r_{j,n_j}$ be the replication events at time t_j . We can use equation 7.2 to write down the following.

$$\begin{aligned}
\mu_{t_j - \epsilon}^{t_j + \delta} &= \frac{1}{N_{t_j + \delta}} \sum_{i=1}^{n_j} \Delta \phi_{r_{j,i}} \\
&= \frac{1}{N_{t_j}} \sum_{i=1}^{n_j} \Delta \phi_{r_{j,i}}
\end{aligned} \tag{B.1}$$

Choosing k as in the proof of theorem 6.3 will lead to the following.

$$\begin{aligned}
\mu_a^{b,k} &= \sum_{t_j \in U} \mu_{t_j - \epsilon}^{t_j + \delta} \\
&= \sum_{t_j \in U} \frac{1}{N_{t_j}} \sum_{i=1}^{n_j} \Delta \phi_{r_{j,i}} \\
&= \sum_{i=1}^n \frac{\Delta \phi_{r_i}}{N_{t_i}}
\end{aligned} \tag{B.2}$$

Because of our choice of k , the same holds for the limit case where we take $k \uparrow \infty$.

□

C Proofs of theorems 8.17 and 8.18

Both proofs are analogous.

Proof. (of theorem 8.17)

$$\begin{aligned}
& \text{Cov}_b^{(K)}(\phi_{\text{anc}_a(j)}, \frac{K(j, b) / \sum_{j \in R_b} K(j, b)}{K(\text{anc}_a(j)) / \sum_{j \in R_b} K(\text{anc}_a(j))} | \text{anc}_a(j)) \\
&= \frac{\sum_{j \in R_b} K(\text{anc}_a(j))}{\sum_{j \in R_b} K(b_j)} \text{Cov}_i(\phi_{\text{anc}_a(j)}, \frac{K(j, b)}{K(\text{anc}_a(j))} | \text{anc}_a(j)) \\
&= \frac{\sum_{j \in R_b} K(\text{anc}_a(j))}{\sum_{j \in R_b} K(b_j)} [\mathbf{E}_b(\frac{K(j, b)\phi_{\text{anc}_a(j)}}{K(\text{anc}_a(j))} | \text{anc}_a(j)) - \mathbf{E}_b(\phi_{\text{anc}_a(j)} | \text{anc}_a(j)) \mathbf{E}_b(\frac{K(j, b)}{K(\text{anc}_a(j))} | \text{anc}_a(j))] \\
&= \frac{\sum_{j \in R_b} K(\text{anc}_a(j))}{\sum_{j \in R_b} K(b_j)} \left[\frac{\sum_{j \in R_b} K(\text{anc}_a(j)) \frac{K(j, b)\phi_{\text{anc}_a(j)}}{K(\text{anc}_a(j))}}{\sum_{j \in R_b} K(\text{anc}_a(j))} - \frac{\sum_{j \in R_b} K(\text{anc}_a(j))\phi_{\text{anc}_a(j)}}{\sum_{j \in R_b} K(\text{anc}_a(j))} \frac{\sum_{j \in R_b} K(\text{anc}_a(j)) \frac{K(j, b)}{K(\text{anc}_a(j))}}{\sum_{j \in R_b} K(\text{anc}_a(j))} \right] \\
&= \frac{\sum_{j \in R_b} K(\text{anc}_a(j)) \frac{K(j, b)\phi_{\text{anc}_a(j)}}{K(\text{anc}_a(j))}}{\sum_{j \in R_b} K(j, b)} - \frac{\sum_{j \in R_b} K(\text{anc}_a(j))\phi_{\text{anc}_a(j)}}{\sum_{j \in R_b} K(\text{anc}_a(j))} \frac{\sum_{j \in R_b} K(\text{anc}_a(j)) \frac{K(j, b)}{K(\text{anc}_a(j))}}{\sum_{j \in R_b} K(j, b)} \\
&= \frac{\sum_{j \in R_b} K(j, b)\phi_{\text{anc}_a(j)}}{\sum_{j \in R_b} K(j, b)} - \frac{\sum_{j \in R_b} K(\text{anc}_a(j))\phi_{\text{anc}_a(j)}}{\sum_{j \in R_b} K(\text{anc}_a(j))} \frac{\sum_{j \in R_b} K(j, b)}{\sum_{j \in R_b} K(j, b)} \\
&= \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)}) - \mathbf{E}_b^{(K)}(\phi_{\text{anc}_a(j)} | \text{anc}_a(j)) \\
&= M_a^{b(K)}
\end{aligned} \tag{C.1}$$

□

Proof. (of theorem 8.17)

$$\begin{aligned}
& \text{Cov}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)}, \frac{K(j, b) / \sum_{j \in R_b} K(j, b)}{K(\text{anc}_a(j)) / \sum_{j \in R_b} K(\text{anc}_a(j))} | \text{anc}_a(j)) \\
&= \frac{\sum_{j \in R_b} K(\text{anc}_a(j))}{\sum_{j \in R_b} K(b_j)} \text{Cov}_i(\phi_j - \phi_{\text{anc}_a(j)}, \frac{K(j, b)}{K(\text{anc}_a(j))} | \text{anc}_a(j)) \\
&= \frac{\sum_{j \in R_b} K(\text{anc}_a(j))}{\sum_{j \in R_b} K(b_j)} [\mathbf{E}_b(\frac{K(j, b)(\phi_j - \phi_{\text{anc}_a(j)})}{K(\text{anc}_a(j))} | \text{anc}_a(j)) - \mathbf{E}_b(\phi_j - \phi_{\text{anc}_a(j)} | \text{anc}_a(j)) \mathbf{E}_b(\frac{K(j, b)}{K(\text{anc}_a(j))} | \text{anc}_a(j))] \\
&= \frac{\sum_{j \in R_b} K(\text{anc}_a(j))}{\sum_{j \in R_b} K(b_j)} \left[\frac{\sum_{j \in R_b} K(\text{anc}_a(j)) \frac{K(j, b)(\phi_j - \phi_{\text{anc}_a(j)})}{K(\text{anc}_a(j))}}{\sum_{j \in R_b} K(\text{anc}_a(j))} - \frac{\sum_{j \in R_b} K(\text{anc}_a(j))(\phi_j - \phi_{\text{anc}_a(j)})}{\sum_{j \in R_b} K(\text{anc}_a(j))} \frac{\sum_{j \in R_b} K(\text{anc}_a(j)) \frac{K(j, b)}{K(\text{anc}_a(j))}}{\sum_{j \in R_b} K(\text{anc}_a(j))} \right] \\
&= \frac{\sum_{j \in R_b} K(\text{anc}_a(j)) \frac{K(j, b)(\phi_j - \phi_{\text{anc}_a(j)})}{K(\text{anc}_a(j))}}{\sum_{j \in R_b} K(j, b)} - \frac{\sum_{j \in R_b} K(\text{anc}_a(j))(\phi_j - \phi_{\text{anc}_a(j)})}{\sum_{j \in R_b} K(\text{anc}_a(j))} \frac{\sum_{j \in R_b} K(\text{anc}_a(j)) \frac{K(j, b)}{K(\text{anc}_a(j))}}{\sum_{j \in R_b} K(j, b)} \\
&= \frac{\sum_{j \in R_b} K(j, b)(\phi_j - \phi_{\text{anc}_a(j)})}{\sum_{j \in R_b} K(j, b)} - \frac{\sum_{j \in R_b} K(\text{anc}_a(j))(\phi_j - \phi_{\text{anc}_a(j)})}{\sum_{j \in R_b} K(\text{anc}_a(j))} \frac{\sum_{j \in R_b} K(j, b)}{\sum_{j \in R_b} K(j, b)} \\
&= \mathbf{E}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)}) - \mathbf{E}_b^{(K)}(\phi_j - \phi_{\text{anc}_a(j)} | \text{anc}_a(j)) \\
&= \kappa_a^{b(K)}
\end{aligned} \tag{C.2}$$

□

D Proof of theorem 9.10

We prove theorem 9.10 under definitions definitions 10.11.

First, we will introduce some lemmas. All of these lemmas are proven by simply writing out all of the definitions and by rearranging terms.

Lemma D.1. Let \mathcal{K} be a weight collection and let $t \in I$. Then the following equality holds.

$$\sum_{K \in \mathcal{K}} |K_t| = N_t \quad (\text{D.1})$$

Proof.

$$\begin{aligned} \sum_{K \in \mathcal{K}} |K_t| &= \sum_{K \in \mathcal{K}} \sum_{i \in R_t} K(i, t) \\ &= \sum_{i \in R_t} \sum_{K \in \mathcal{K}} K(i, t) \\ (\text{since } \mathcal{K} \text{ is a weight collection}) &= \sum_{i \in R_t} \\ &= N_t \end{aligned} \quad (\text{D.2})$$

□

Lemma D.2. Let f be any function of replicators at time a . Then the following equality holds.

$$\mathbf{E}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(f) | K_a] = \mathbf{E}_a(f) \quad (\text{D.3})$$

Proof.

$$\begin{aligned} \mathbf{E}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(f) | K_a] &= \mathbf{E}_{\mathcal{K}}\left[\frac{\sum_{i \in R_a} K(i, a) f(i)}{|K_a|} \mid K_a\right] \\ &= \frac{\sum_{K \in \mathcal{K}} \frac{\sum_{i \in R_a} K(i, a) f(i)}{|K_a|} |K_a|}{\sum_{K \in \mathcal{K}} |K_a|} \\ &= \frac{\sum_{K \in \mathcal{K}} \sum_{i \in R_a} K(i, a) f(i)}{\sum_{K \in \mathcal{K}} \sum_{i \in R_a} K(i, a)} \\ &= \frac{\sum_{i \in R_a} (\sum_{K \in \mathcal{K}} K(i, a)) f(i)}{\sum_{i \in R_a} \sum_{K \in \mathcal{K}} K(i, a)} \\ (\text{since } \mathcal{K} \text{ is a weight collection}) &= \frac{\sum_{i \in R_a} f(i)}{i \in R_a} \\ &= \frac{\sum_{i \in R_a} f(i)}{N_a} \\ &= \mathbf{E}_a(f) \end{aligned} \quad (\text{D.4})$$

□

Lemma D.3. Let f be any function of replicators at time a and let m be any function of weight functions. Then the following equality holds.

$$\mathbf{E}_{\mathcal{K}}[m(K) \mathbf{E}_a^{(K)}(f w_a^{b(K)}) | K_a | \overline{W}_a^b{}^{(K)}] = \mathbf{E}_{\mathcal{K}}[m(K) \mathbf{E}_a^{(K)}(f w_a^b) | K_a] \quad (\text{D.5})$$

Proof.

$$\begin{aligned}
& \mathbf{E}_{\mathcal{K}}[m(K)\mathbf{E}_a^{(K)}(fw_a^{b(K)})||K_a|\overline{W}_a^{b(K)}] \\
&= \mathbf{E}_{\mathcal{K}}[m(K)\mathbf{E}_a^{(K)}(f\frac{W_a^b}{\overline{W}_a^{b(K)}})||K_a|\overline{W}_a^{b(K)}] \\
&= \mathbf{E}_{\mathcal{K}}[m(K)\frac{\sum_{i \in R_a} K(i,a)f(i)W_a^b(i)}{|K_a|\overline{W}_a^{b(K)}}||K_a|\overline{W}_a^{b(K)}] \\
&= \frac{\sum_{K \in \mathcal{K}} m(K)\frac{\sum_{i \in R_a} K(i,a)f(i)W_a^b(i)}{|K_a|\overline{W}_a^{b(K)}}|K_a|\overline{W}_a^{b(K)}}{\sum_{K \in \mathcal{K}} |K_a|\overline{W}_a^{b(K)}} \\
&= \frac{\sum_{K \in \mathcal{K}} m(K)\sum_{i \in R_a} K(i,a)f(i)W_a^b(i)}{\sum_{K \in \mathcal{K}} |K_a|\overline{W}_a^{b(K)}} \\
&= \frac{\sum_{K \in \mathcal{K}} m(K)\sum_{i \in R_a} K(i,a)f(i)W_a^b(i)/\sum_{K \in \mathcal{K}} |K_a|}{\sum_{K \in \mathcal{K}} |K_a|\overline{W}_a^{b(K)}/\sum_{K \in \mathcal{K}} |K_a|} \\
\text{(by lemma D.1)} &= \frac{\sum_{K \in \mathcal{K}} m(K)\sum_{i \in R_a} K(i,a)f(i)W_a^b(i)/N_a}{\mathbf{E}_{\mathcal{K}}[\overline{W}_a^{b(K)}||K_a|]} \\
\text{(by lemma D.2)} &= \frac{\sum_{K \in \mathcal{K}} m(K)\sum_{i \in R_a} K(i,a)f(i)W_a^b(i)/N_a}{\overline{W}_a^b} \\
&= \frac{\sum_{K \in \mathcal{K}} m(K)\sum_{i \in R_a} K(i,a)f(i)W_a^b(i)/\overline{W}_a^b}{N_a} \\
&= \frac{\sum_{K \in \mathcal{K}} m(K)\sum_{i \in R_a} K(i,a)f(i)w_a^b(i)}{N_a} \\
\text{(by lemma D.1)} &= \frac{\sum_{K \in \mathcal{K}} m(K)\frac{\sum_{i \in R_a} K(i,a)f(i)w_a^b(i)}{|K_a|}|K_a|}{\sum_{K \in \mathcal{K}} |K_a|} \\
&= \mathbf{E}_{\mathcal{K}}[m(K)\frac{\sum_{i \in R_a} K(i,a)f(i)w_a^b(i)}{|K_a|}||K_a|] \\
&= \mathbf{E}_{\mathcal{K}}[m(K)\mathbf{E}_a^{(K)}(f(i)w_a^b(i))||K_a|]
\end{aligned} \tag{D.6}$$

□

We are now ready to prove theorem 9.10.

Proof. (of theorem 9.10, using definitions 10.11)

$$\begin{aligned}
S_{a,\text{inter}}^b + S_{a,\text{intra}}^b &= \text{Cov}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(\phi), \mathbf{E}_a^{(K)}(w_a^b)||K_a|] + \mathbf{E}_{\mathcal{K}}[S_a^{b(K)}||K_a|\overline{W}_a^{b(K)}] \\
&= \text{Cov}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(\phi), \mathbf{E}_a^{(K)}(w_a^b)||K_a|] + \mathbf{E}_{\mathcal{K}}[\text{Cov}_a^{(K)}(\phi, w_a^{b(K)})||K_a|\overline{W}_a^{b(K)}] \\
&= \mathbf{E}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(\phi)\mathbf{E}_a^{(K)}(w_a^b)||K_a|] - \mathbf{E}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(\phi)||K_a|]\mathbf{E}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(w_a^b)||K_a|] \\
&\quad + \mathbf{E}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(\phi w_a^b) - \mathbf{E}_a^{(K)}(\phi)\mathbf{E}_a^{(K)}(w_a^b)||K_a|\overline{W}_a^{b(K)}] \\
\text{(by lemma D.3)} &= \mathbf{E}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(\phi)\mathbf{E}_a^{(K)}(w_a^b)||K_a|] - \mathbf{E}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(\phi)||K_a|]\mathbf{E}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(w_a^b)||K_a|] \\
&\quad + \mathbf{E}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(\phi w_a^b)||K_a|] - \mathbf{E}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(\phi)\mathbf{E}_a^{(K)}(w_a^b)||K_a|] \\
&= \mathbf{E}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(\phi w_a^b)||K_a|] - \mathbf{E}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(\phi)||K_a|]\mathbf{E}_{\mathcal{K}}[\mathbf{E}_a^{(K)}(w_a^b)||K_a|] \\
\text{(by lemma D.2)} &= \mathbf{E}_a(\phi w_a^b) - \mathbf{E}_a(\phi)\mathbf{E}_a(w_a^b) \\
&= \text{Cov}_a(\phi, w_a^b) \\
&= S_a^b
\end{aligned} \tag{D.7}$$

□

E The meaning of $\widehat{M_a^b + \kappa_a^b}$, $\widehat{M_a^b}$ and $\widehat{\kappa_a^b}$

As a first attempt to get a better intuitive understanding of the terms $\widehat{M_a^b + \kappa_a^b}$, $\widehat{M_a^b}$ and $\widehat{\kappa_a^b}$, we will rewrite them in covariance terms. But first we will introduce a new definition:

Definition E.1.

$$\Phi_a^b(K) \equiv \frac{|K_a| \overline{W_a^b}^{(K)}}{|K_b|} = \frac{\sum_{i \in R_a} K(i) W_a^b(i)}{\sum_{j \in R_b} K(j)} = \frac{\sum_{j \in R_b} K(\text{anc}_a(j))}{\sum_{j \in R_b} K(j)} \quad (\text{E.1})$$

This term will become important, so we will focus on its meaning for a while. To make our reasoning more intuitive, suppose that there are discrete groups and weight functions are defined as in equation 10.5. Let g_j be a group. If as many replicators migrate into group g_j as migrate out of the group, the denominator and numerator in equation E.1 will be equal to each other and $\Phi_a^b(K_j) = 1$. If there is net immigration into g_j , the denominator will be bigger than the numerator, so then $\Phi_a^b(K_j) < 1$; and if there is net emigration out of g_j , it will be smaller than the numerator, so then $\Phi_a^b(K_j) > 1$. More precisely, if group g_j is C times bigger than would be the case if all weight functions were constant in time, the denominator in equation E.1 will be C times bigger than the numerator, so then $\Phi_a^b(K_j) = \frac{1}{C}$. As such, one can interpret $\Phi_a^b(K_j)$ as the ‘inverse of the growth factor due to migration of g_j ’.

Now that we have an understanding of the term $\Phi_a^b(K)$, it is time to introduce our theorems.

Theorem E.2.

$$\widehat{M_a^b + \kappa_a^b} = \text{Cov}_b(\phi_j, \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K)) \quad (\text{E.2})$$

Theorem E.3.

$$\widehat{M_a^b} = \text{Cov}_b(\phi_{\text{anc}_a(j)}, \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K)) \quad (\text{E.3})$$

Theorem E.4.

$$\widehat{\kappa_a^b} = \text{Cov}_b(\phi_j - \phi_{\text{anc}_a(j)}, \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K)) \quad (\text{E.4})$$

To prove these theorems, we will make use the following respective lemmas.

Lemma E.5.

$$\widehat{M_a^b + \kappa_a^b} = \mathbf{E}_b(\phi_j \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K)) - \overline{\phi_b} \quad (\text{E.5})$$

Lemma E.6.

$$\widehat{M_a^b} = \mathbf{E}_b(\phi_j \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K)) - \overline{\phi_b} \quad (\text{E.6})$$

Lemma E.7.

$$\widehat{\kappa_a^b} = \mathbf{E}_b((\phi_j - \phi_{\text{anc}_a(j)}) \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K)) - \overline{\phi_b} \quad (\text{E.7})$$

We will only show a proof of lemma E.5 and theorem E.2, because the proofs for the other two lemmas and theorems are analogous. To get from the proof of lemma E.5 and theorem E.2 to the other proofs, one has to replace the term ϕ_j with $\phi_{\text{anc}_a(j)}$ and $\phi_j - \phi_{\text{anc}_a(j)}$, respectively.

Proof. (of lemma E.5)

$$\begin{aligned}
\widehat{M_a^b + \kappa_a^b} &= \mathbf{E}_{\mathcal{K}}[M_a^{b(K)} + \kappa_a^{b(K)} | K_a | \overline{W_a^b}^{(K)}] \\
&= \mathbf{E}_{\mathcal{K}}[M_a^{b(K)} + \kappa_a^{b(K)} | K_b | \Phi_a^b(K)] \\
&= \frac{1}{N_b} \sum_{K \in \mathcal{K}} |K_b| \Phi_a^b(K) (M_a^{b(K)} + \kappa_a^{b(K)}) \\
&= \frac{1}{N_b} \sum_{K \in \mathcal{K}} |K_b| \Phi_a^b(K) (\mathbf{E}_b^{(K)}(\phi) - \mathbf{E}_b^{(K)}(\phi_j | \text{anc}_a(j))) \\
&= \frac{1}{N_b} \sum_{K \in \mathcal{K}} |K_b| \Phi_a^b(K) \left(\frac{\sum_{j \in R_b} K(j) \phi_j}{|K_b|} - \frac{\sum_{j \in R_b} K(\text{anc}_a(j)) \phi_j}{\sum_{j \in R_b} K(\text{anc}_a(j))} \right) \\
&= \frac{1}{N_b} \sum_{K \in \mathcal{K}} |K_b| \Phi_a^b(K) \sum_{j \in R_b} \left(\frac{K(j) \phi_j}{|K_b|} - \frac{K(\text{anc}_a(j)) \phi_j}{\sum_{i \in R_b} K(\text{anc}_a(i))} \right) \\
&= \frac{1}{N_b} \sum_{j \in R_b} \phi_j \sum_{K \in \mathcal{K}} |K_b| \Phi_a^b(K) \left(\frac{K(j)}{|K_b|} - \frac{K(\text{anc}_a(j))}{\sum_{i \in R_b} K(\text{anc}_a(i))} \right) \\
&= \frac{1}{N_b} \sum_{j \in R_b} \phi_j \sum_{K \in \mathcal{K}} (K(j, b) \Phi_a^b(K) - \frac{\Phi_a^b(K) |K_b| K(\text{anc}_a(j))}{\sum_{i \in R_b} K(\text{anc}_a(i))}) \\
&= \frac{1}{N_b} \sum_{j \in R_b} \phi_j \sum_{K \in \mathcal{K}} (K(j, b) \Phi_a^b(K) - \frac{\Phi_a^b(K) K(\text{anc}_a(j))}{\Phi_a^b(K)}) \\
&= \frac{1}{N_b} \sum_{j \in R_b} \phi_j \sum_{K \in \mathcal{K}} (K(j, b) \Phi_a^b(K) - K(\text{anc}_a(j))) \\
&= \frac{1}{N_b} \sum_{j \in R_b} \phi_j \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K) - \frac{1}{N_b} \sum_{j \in R_b} \phi_j \sum_{K \in \mathcal{K}} K(\text{anc}_a(j)) \\
&= \frac{1}{N_b} \sum_{j \in R_b} \phi_j \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K) - \frac{1}{N_b} \sum_{j \in R_b} \phi_j \\
&= \mathbf{E}_b(\phi_j \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K)) - \overline{\phi_b}
\end{aligned} \tag{E.8}$$

□

Proof. (of theorem E.2) Note the following.

$$\begin{aligned}
\mathbf{E}_b\left(\sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K)\right) &= \frac{1}{N_b} \sum_{j \in R_b} \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K) \\
&= \frac{1}{N_b} \sum_{K \in \mathcal{K}} \left(\sum_{j \in R_b} K(j, b) \Phi_a^b(K) \right) \\
&= \frac{1}{N_b} \sum_{K \in \mathcal{K}} \sum_{j \in R_b} K(\text{anc}_a(j)) \\
&= \frac{1}{N_b} \sum_{j \in R_b} \sum_{K \in \mathcal{K}} K(\text{anc}_a(j)) \\
&= \frac{1}{N_b} \sum_{j \in R_b} 1 \\
&= 1
\end{aligned} \tag{E.9}$$

Now we can combine our previous findings to show the following:

$$\begin{aligned}
\text{Cov}_b(\phi_j, \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K)) &= \mathbf{E}_b(\phi_j \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K)) - \mathbf{E}_b(\phi_j) \mathbf{E}_b\left(\sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K)\right) \\
&\text{(using equation E.9)} = \mathbf{E}_b(\phi_j \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K)) - \overline{\phi_b} \\
&\text{(using lemma E.5)} = \widehat{M_a^b + \kappa_a^b}
\end{aligned} \tag{E.10}$$

□

Corollary E.8. *If $\Phi_a^b(K) = 1$ for all weight functions K , then the following holds.*

$$\widehat{M_a^b + \kappa_a^b} = \widehat{M_a^b} = \widehat{\kappa_a^b} = 0 \quad (\text{E.11})$$

Proof. Suppose $\Phi_a^b(K) = 1$ for all weight functions K . Then for all weight functions K :

$$\sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K) = \sum_{K \in \mathcal{K}} K(j, b) = 1 \quad (\text{E.12})$$

Since the covariance with any constant is equal to 0, all the covariance terms in theorems E.2, E.3 and E.4 are equal to 0. □

Note that $\Phi_a^b(K) = 1$ if and only if $\sum_{j \in R_b} K(j, b) = \sum_{j \in R_b} K(\text{anc}_a(j))$. In the case of discrete groups, this would mean that migration has had no effect on group size.

We will now focus our attention on the interpretations of theorems E.2, E.3 and E.4.

The left sides of the covariance terms in theorems E.2, E.3 and E.4 are straightforward, but the right hand sides not so much. We know that $\sum_{K \in \mathcal{K}} K(j, b)$ adds up to 1. We are essentially doing this summation, except that we weigh all $K(j, b)$ terms by the term $\Phi_a^b(K)$. If and only if migration decreases the size of a group g_j , the term $\Phi_a^b(K)$ is larger than 1. As such, the migration terms are positive if and only if *replicators with a relatively high phenotype, more so than replicators with a relatively low phenotype, tend to be at time b in groups of which the size has decreased due to migration events in the time interval $(a, b]$* . On average, replicators that migrate have a tendency to *not* end up in groups of which the size has decreased due to migration events, since their own migration is contributing to the increase of the group size of whatever group they are migrating into. As such, in many cases the migration terms will be positive if replicators tend to migrate less the higher their phenotype is.

Still, these terms are not intuitively easy to understand. I will proceed by giving some examples in order to improve intuition.

Example 10. Let us, again, consider discrete groups, and weight functions as defined in equation 10.5. Suppose that in between times a and b , there is only 1 migration event: namely a replicator migrates from group g_1 into group g_2 . What would the effect of this single migration event be on the average of the migration terms? Note that

$$|K_{1,b}| = |K_{1,a}| \overline{W_a^b}^{(K_1)} - 1 \quad (\text{E.13})$$

since 1 replicator has migrated out of group g_1 , and

$$|K_{2,b}| = |K_{2,a}| \overline{W_a^b}^{(K_2)} + 1 \quad (\text{E.14})$$

since 1 replicator has migrated into it. Now we can use lemma E.5 to calculate the following.

$$\begin{aligned}
& \widehat{M_a^b + \kappa_a^b} \\
&= \mathbf{E}_b(\phi_j \sum_{i=1}^2 K_i(j, b) \Phi_a^b(K)) - \overline{\phi_b} \\
&= \mathbf{E}_b(\phi_j \sum_{i=1}^2 \frac{K_i(j, b) |K_{i,a}| \overline{W_a^b}^{(K_i)}}{|K_{i,b}|}) - \frac{1}{N_b} \sum_{j \in R_b} \phi_j \\
&= \frac{1}{N_b} (\sum_{j \in R_b} \phi_j \sum_{i=1}^2 \frac{K_i(j, b) |K_{i,a}| \overline{W_a^b}^{(K_i)}}{|K_{i,b}|} - \sum_{j \in R_b} (K_1(j, b) + K_2(j, b)) \phi_j) \\
&= \frac{1}{N_b} (\sum_{j \in R_b} \phi_j (\frac{K_1(j, b) |K_{1,a}| \overline{W_a^b}^{(K_1)}}{|K_{1,b}|} + \frac{K_2(j, b) |K_{2,a}| \overline{W_a^b}^{(K_2)}}{|K_{2,b}|}) - \sum_{j \in R_b} (K_1(j, b) + K_2(j, b)) \phi_j) \quad (\text{E.15}) \\
&= \frac{1}{N_b} (\sum_{j \in R_b} \phi_j (\frac{K_1(j, b) (|K_{1,b}| + 1)}{|K_{1,b}|} + \frac{K_2(j, b) (|K_{2,b}| - 1)}{|K_{2,b}|}) - \sum_{j \in R_b} (K_1(j, b) + K_2(j, b)) \phi_j) \\
&= \frac{1}{N_b} (\sum_{j \in R_b} \phi_j (\frac{K_1(j, b) (|K_{1,b}| + 1)}{|K_{1,b}|} - K_1(j, b) + \frac{K_2(j, b) (|K_{2,b}| - 1)}{|K_{2,b}|} - K_2(j, b))) \\
&= \frac{1}{N_b} (\sum_{j \in R_b} \phi_j (\frac{K_1(j, b)}{|K_{1,b}|} - \frac{K_2(j, b)}{|K_{2,b}|})) \\
&= \frac{1}{N_b} (\overline{\phi_b}^{(K_1)} - \overline{\phi_b}^{(K_2)})
\end{aligned}$$

Put in words, if there is a single migration event in which a replicator moves from a group with a high (low) average phenotype into a group with a low (high) average phenotype, the average of the migration terms will be positive (negative). We can understand this with our result from equation E.2. Suppose group g_1 has a higher average phenotype than group g_2 , and a replicator moves from group g_1 into group g_2 . Then the replicators in group g_1 see the size of their group decrease due to migration, and the replicators in group g_2 see the size of their group increase due to migration. Since the replicators in group g_1 have, on average, a higher phenotype than the replicators in group g_2 , the covariance between phenotype and ‘being in groups of which the size has decreased due to migration events’ is positive.

There is a big caveat in the result of equation E.15, though: the averages $\overline{\phi_b}^{(K_1)}$ and $\overline{\phi_b}^{(K_2)}$ are calculated after the migration has already happened. As an example of a case where this is important, suppose that groups g_1 and g_2 have the same average phenotype at time a and that in between time a and b , a replicator with a particularly high phenotype migrates from group g_1 into group g_2 . Then at time b , group g_1 will have a lower average phenotype than before and group g_2 will have a higher average phenotype than before, so the average of the migration terms will be *negative*. We can understand this phenomenon in terms of theorem E.2, too. A replicator that migrates will negatively contribute to the decrease in size of the group it migrates into, so in this example, phenotype negatively correlates with being at time b in a group of which the size has decreased due to migration in the time interval $(a, b]$.

Example 11. Let us now look at another example. Suppose there are $m \geq 2$ groups, g_1 up to g_m , and every weight function is defined as in equation 10.5. One replicator has phenotype $\phi + \epsilon$ with $\epsilon > 0$. At time a , it is in group g_1 , and at time b , it has migrated into group g_2 . All other replicators have phenotype ϕ and neither reproduce nor die (so $\kappa_a^b(K_1) = \kappa_a^b(K_2) = 0$). Then $M_a^b(K_1)$ equals the following:

$$\begin{aligned}
\overline{\phi_b}^{(K_1)} - \overline{\phi_a}^{(K_1)} &= \frac{|K_{1,b}| \phi}{|K_{1,b}|} - \frac{(|K_{1,a}| - 1) \phi + \phi + \epsilon}{|K_{1,a}|} \\
&= -\frac{\epsilon}{|K_{1,a}|}
\end{aligned} \quad (\text{E.16})$$

Also, $M_a^b(K_2)$ equals the following:

$$\begin{aligned}
\overline{\phi_b}^{(g_2)} - \overline{\phi_a}^{(g_2)} &= \frac{(|g_2|)_b - 1}{|K_{2,b}|} \phi + \phi + \epsilon - \frac{|K_{2,a}| \phi}{|K_{2,a}|} \\
&= \frac{\epsilon}{|K_{2,b}|}
\end{aligned} \quad (\text{E.17})$$

At the same time, for all $j > 2$, $M_a^{b(K_j)}$ equals the following:

$$\begin{aligned}\overline{\phi_b}^{(K_2)} - \overline{\phi_a}^{(K_2)} &= \phi - \phi \\ &= 0\end{aligned}\tag{E.18}$$

We can use this to find an expression for \widehat{M}_a^b :

$$\begin{aligned}\widehat{M}_a^b &= \mathbf{E}_{\mathcal{K}}[M_a^{b(K_j)} | |K_{j,a}|] \\ &= \frac{1}{N_b} \sum_{K \in \mathcal{K}} |K_{j,a}| M_a^{b(K_j)} \\ &= \frac{1}{N_b} (|K_{1,a}| M_a^{b(g_1)} + |K_{2,a}| M_a^{b(g_2)} + \sum_{j=3}^m |K_{j,a}| M_a^{b(K_j)}) \\ &= \frac{1}{N_b} (|K_{1,a}| M_a^{b(g_1)} + |K_{2,a}| M_a^{b(g_2)}) \\ &= -\epsilon + \frac{|K_{2,a}|}{|K_{2,b}|} \epsilon \\ &= \frac{|K_{2,a}| - |K_{2,b}|}{|K_{2,b}|} \epsilon\end{aligned}\tag{E.19}$$

This demonstrates that a replicator with a high phenotype that migrates into a group that increases in size due to migration, will cause the migration term to decrease. This also pretty much follows from equation E.2. If the one replicator who is migrating and who has a higher than average phenotype moves into a group that increases in size due to migration, then the covariance between phenotype and ‘being in groups of which the size has decreased due to migration events’ is negative. Note that also if everyone is migrating randomly, this covariance is more likely to be negative than positive, as a migrating replicator contributes to the increase of the group size of whatever group it migrates into. In this particular example, no parameter of group g_1 came into the equation, since I gave its replicators the same phenotype as the replicators in group g_2 initially had.

As we have seen, the migration term is the covariance between phenotype and ‘tendency to be at time b in groups of which the size has decreased due to migration events in the time interval $(a, b]$ ’. For all replicators that migrate, the decrease in group size due to migration effects is weakened by their own migration. It would be nice if we could split up the term $\Phi_a^b(K)$, which describes the ‘tendency to be at time b in groups of which the size has decreased due to migration events in the time interval $(a, b]$ ’, into the covariance between phenotype and ‘tendency to be at time b in groups of which the size has decreased due to migration events of *other* replicators in the time interval $(a, b]$ ’ and (minus) the covariance between phenotype and ‘tendency to migrate *yourself* in the time interval $(a, b]$ ’. As it turns out, we can do this, as the following definitions and theorem show.

Definitions E.9. We define the following for all weight functions K and $j \in R_b$.

$$\Phi_a^b(K, j-) \equiv \frac{\sum_{i \in R_b, i \neq j} K(\text{anc}_a(i)) + K(j, b)}{|K_b|}\tag{E.20}$$

$$\Phi_a^b(K, j+) \equiv \frac{K(\text{anc}_a(j)) - K(j, b)}{|K_b|}\tag{E.21}$$

Theorem E.10.

$$\widehat{M}_a^b + \kappa_a^b = \text{Cov}_b(\phi_j, \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K, j-)) + \text{Cov}_b(\phi_j, \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K, j+))\tag{E.22}$$

Proof. Let $j \in R_b$. We have the following equality.

$$\begin{aligned}\Phi_a^b(K) &= \frac{\sum_{i \in R_b} K(\text{anc}_a(i))}{|K_b|} \\ &= \frac{\sum_{i \in R_b, i \neq j} K(\text{anc}_a(i)) + K(j, b)}{|K_b|} + \frac{K(\text{anc}_a(j)) - K(j, b)}{|K_b|} \\ &= \Phi_a^b(K, j-) + \Phi_a^b(K, j+)\end{aligned}\tag{E.23}$$

From this, the following can be concluded.

$$\begin{aligned}
\widehat{M}_a^b + \widehat{\kappa}_a^b &= \text{Cov}_b(\phi, \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K)) \\
&= \text{Cov}_b(\phi, \sum_{K \in \mathcal{K}} (K(j, b) \Phi_a^b(K, j-) + (K(j, b) \Phi_a^b(K, i+))) \\
&= \text{Cov}_b(\phi, \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K, j-)) + \text{Cov}_b(\phi, \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K, j+))
\end{aligned} \tag{E.24}$$

□

Remark E.11. As always, analogous theorems exist for \widehat{M}_a^b and $\widehat{\kappa}_a^b$.

The new terms can be interpreted as follows.

The term $\Phi_a^b(K, j-)$ is the same as $\Phi_a^b(K)$, except that it changes the term $K(\text{anc}_a(j))$ into $K(j, b)$. As such, $\Phi_a^b(K, j-)$ is the same as $\Phi_a^b(K)$ except that it treats the ancestor of replicator j at time a as if it had already been at the position of its descendant j at time b . This essentially means that it filters out the effect of the migration of (the ancestors of) replicator j but correctly identifies its current position. As such, $K(j, b) \Phi_a^b(K, j-)$ is indeed the ‘tendency to be at time b in groups of which the size has decreased due to migration events of *other* replicators in the time interval $(a, b]$ ’.

The term $\Phi_a^b(K, j+)$ describes the difference in position between replicator j and its ancestor at time a . Let us study what this term means with help of some examples.

Example 12. Suppose that replicator j has not migrated at all, i.e. $\text{anc}_a(j) = K(j, b)$ for all weight functions K . Then $\Phi_a^b(K, j+) = 0$ for all K , so it also follows that

$$\sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K, j+) = 0 \tag{E.25}$$

and since a covariance of something with a constant is always 0,

$$\text{Cov}_b(\phi, \sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K, j+)) \tag{E.26}$$

which is to be expected if replicator j has not migrated.

Example 13. Now let us assume that replicator j (or its ancestor(s) after time a) has migrated. Let us first assume that all weight functions are defined as in equation 10.5. This means that for some i' , $K_{i'}(j, b) = 1$, $K_i(j, b) = 0$ for all $i \neq i'$, and for some $i'' \neq i'$, $K_{i''}(\text{anc}_a(j)) = 1$, and $K_i(\text{anc}_a(j)) = 0$ for all $i \neq i''$. Then

$$\begin{aligned}
\sum_{K_i \in \mathcal{K}} K_i(j, b) \Phi_a^b(K_i, j+) &= \sum_{K_i \in \mathcal{K}} \frac{K_i(\text{anc}_a(j)) - K_i(j, b)}{|K_{ib}|} K_i(j, b) \\
(\text{since } K_i(j, b) = 0 \text{ for all } i \neq i') &= \frac{K_{i'}(\text{anc}_a(j)) - K_{i'}(j, b)}{|K_{i'b}|} K_{i'}(j, b) \\
(\text{since } K_{i'}(\text{anc}_a(j)) = 0 \text{ and } K_{i'}(j, b) = 1) &= -\frac{1}{|K_{i'b}|} \\
&< 0
\end{aligned} \tag{E.27}$$

which makes sense to be a negative number, since this term is supposed to capture the inverse of the ‘tendency to migrate yourself’.

However, if weight functions are *not* defined as in equation 10.5, then in some instances $\Phi_a^b(g_j, i+)$ is *not* negative if replicator i migrates. The next example will demonstrate this.

Example 14. Suppose that for some replicator j and some weight functions K', K'' the following holds: $K'(j, b) = \frac{2}{3}$, $K''(j, b) = \frac{1}{3}$, $K'(\text{anc}_a(j)) = \frac{1}{3}$, $K''(\text{anc}_a(j)) = \frac{2}{3}$ and $K(j) = K(\text{anc}_a(j)) = 0$ for all $j \notin \{j', j''\}$. Then

$$\begin{aligned}
\sum_{K \in \mathcal{K}} K(j, b) \Phi_a^b(K, j+) &= \sum_{K \in \mathcal{K}} \frac{K(\text{anc}_a(j)) - K(j, b)}{|K_b|} K(j, b) \\
&= \frac{K'(\text{anc}(b_i, a)) - K'(b_i)}{|K'_b|} K'(b_i) + \frac{K''(\text{anc}(b_i, a)) - K''(b_i)}{|K''_b|} K''(b_i) \\
&= \frac{\frac{1}{3} - \frac{2}{3}}{|K'_b|} 2 + \frac{\frac{2}{3} - \frac{1}{3}}{|K''_b|} 1 \\
&= \frac{1}{9} \left(\frac{1}{|K''_b|} - \frac{2}{|K'_b|} \right)
\end{aligned} \tag{E.28}$$

which is smaller than 0 if $|K'_b| = |K''_b|$, but *bigger* than 0 if group $|K'_b| > 2|K''_b|$. With nondiscrete groups, therefore, the term $\sum_{K \in \mathcal{K}} \frac{K(j, b)}{\Phi_a^b(K, j+)}$ is harder to interpret; due to weighing, the term becomes bigger for replicators that have a tendency to migrate into bigger groups than they came from.

F Proof of theorem 12.3 and corollary 12.4

Large parts of the beginning of the proof of theorem 12.3 are analogous to parts from multiple proofs we have already given. We will go over these parts more quickly than over the rest of the proof.

Proof. (of theorem 12.3)

We will start by using an extension to lemma 4.2. Under the same notation as used in this lemma, the following equation holds.

$$\begin{aligned}
S_a^{b(K)} &= \frac{1}{|K_a| \overline{W_a^b}} \left(\sum_{i=1}^n K(\text{anc}_a(r_i)) \phi_{\text{anc}_a(r_i)} - \sum_{j=1}^m K(\text{anc}_a(d_j)) \phi_{\text{anc}_a(d_j)} + (|K_a| - |K_a| \overline{W_a^b}) \overline{\phi_a} \right) \\
&= \frac{1}{|K_a| \overline{W_a^b}} \left(\sum_{i=1}^n K(\text{anc}_a(r_i)) \phi_{\text{anc}_a(r_i)} - \sum_{j=1}^m K(\text{anc}_a(d_j)) \phi_{\text{anc}_a(d_j)} + |K_a| (1 - \overline{W_a^b}) \overline{\phi_a} \right)
\end{aligned} \tag{F.1}$$

This can be verified by precisely following equations 4.2 and 2.10, except adding weight functions at the appropriate places, exchanging N_a for $|K_a|$, and N_b for $|K_a| \overline{W_a^b}$.

Now let $U, \epsilon^*, t_j, \epsilon, \delta$ as in the proof of theorem 6.3. For the same reasons why lemma 4.2 can be used to show equation A.2 to hold, we can use equation F.1 to show the following (using the same notation):

$$\begin{aligned}
&S_{t_j - \epsilon}^{t_j + \delta(K)} \\
&= \frac{1}{|K_{t_j - \epsilon}| \overline{W_{t_j - \epsilon}^{t_j + \delta}}} \left(\sum_{i=1}^{n_j} K(\text{anc}_{t_j - \epsilon}(r_{j,i})) \phi_{\text{anc}_{t_j - \epsilon}(r_{j,i})} - \sum_{i=1}^{m_j} K(\text{anc}_{t_j - \epsilon}(d_{j,i})) \phi_{\text{anc}_{t_j - \epsilon}(d_{j,i})} + |K_{t_j - \epsilon}| (1 - \overline{W_{t_j - \epsilon}^{t_j + \delta}}) \overline{\phi_{t_j - \epsilon}} \right)
\end{aligned} \tag{F.2}$$

Since there are no birth and death events in the time interval $[t_j - \epsilon, t_j]$, we have $\phi_{\text{anc}_{t_j - \epsilon}(r_{j,i})} = \phi_{r_{j,i}}$ and $\phi_{\text{anc}_{t_j - \epsilon}(d_{j,i})} = \phi_{d_{j,i}}$. A such, the following holds.

$$S_{t_j - \epsilon}^{t_j + \delta(K)} = \frac{1}{|K_{t_j - \epsilon}| \overline{W_{t_j - \epsilon}^{t_j + \delta}}} \left(\sum_{i=1}^{n_j} K(\text{anc}_{t_j - \epsilon}(r_{j,i})) \phi_{r_{j,i}} - \sum_{i=1}^{m_j} K(\text{anc}_{t_j - \epsilon}(d_{j,i})) \phi_{d_{j,i}} + |K_{t_j - \epsilon}| (1 - \overline{W_{t_j - \epsilon}^{t_j + \delta}}) \overline{\phi_{t_j - \epsilon}} \right) \tag{F.3}$$

In the proof of lemma 4.2 we used that if k is a replicator that is living at a time a , and $|C_{a_k}^b| - |D_{a_k}^b|$ are the respective number of birth and death events in its lineage in $(a, b]$, then $W_a^b(k) = 1 + |C_{a_k}^b| - |D_{a_k}^b|$. We can derive the following expressions. From the fact that there are no replication and death events in the time interval $(t_j, \delta]$ follows the following:

$$\begin{aligned}
\overline{W_{t_j-\epsilon}^{t_j+\delta}} &= \frac{1}{|K_{t_j-\epsilon}|} \sum_{i \in R_{t_j-\epsilon}} K(\text{anc}_{t_j-\epsilon}(i)) W_{t_j-\epsilon}^{t_j+\delta}(i) \\
&= \frac{1}{|K_{t_j-\epsilon}|} \sum_{i \in R_{t_j-\epsilon}} K(\text{anc}_{t_j-\epsilon}(i)) (1 + |C_{t_j-\epsilon_i}^{t_j+\delta}| - |D_{t_j-\epsilon_i}^{t_j+\delta}|) \\
&= \frac{1}{|K_{t_j-\epsilon}|} \sum_{i \in R_{t_j-\epsilon}} K(\text{anc}_{t_j-\epsilon}(i)) (1 + |C_{t_j-\epsilon_i}^{t_j}| - |D_{t_j-\epsilon_i}^{t_j}|) \\
&= \overline{W_{t_j-\epsilon}^{t_j}}
\end{aligned} \tag{F.4}$$

Also note the following:

$$\begin{aligned}
\sum_{i \in R_{t_j-\epsilon}} K(\text{anc}_{t_j-\epsilon}(i)) W_{t_j-\epsilon}^{t_j+\delta}(i) &= \sum_{i \in R_{t_j-\epsilon}} K(\text{anc}_{t_j-\epsilon}(i)) (1 + |C_{t_j-\epsilon_i}^{t_j+\delta}| - |D_{t_j-\epsilon_i}^{t_j+\delta}|) \\
&= |K_{t_j-\epsilon}| + \sum_{i \in R_{t_j-\epsilon}} K(\text{anc}_{t_j-\epsilon}(i)) |C_{t_j-\epsilon_i}^{t_j+\delta}| - \sum_{i \in R_{t_j-\epsilon}} K(\text{anc}_{t_j-\epsilon}(i)) |D_{t_j-\epsilon_i}^{t_j+\delta}| \\
&= |K_{t_j-\epsilon}| + \sum_{i=1}^{n_j} K(\text{anc}_{t_j-\epsilon}(r_{j,i})) - \sum_{i=1}^{m_j} K(\text{anc}_{t_j-\epsilon}(d_{j,i}))
\end{aligned} \tag{F.5}$$

With this in mind, we will rewrite equation F.3.

$$\begin{aligned}
&S_{t_j-\epsilon}^{t_j}(K) \\
&= \frac{1}{|K_{t_j-\epsilon}| \overline{W_{t_j-\epsilon}^{t_j+\delta}}} \left(\sum_{i=1}^{n_j} K(\text{anc}_{t_j-\epsilon}(r_{j,i})) \phi_{r_{j,i}} - \sum_{i=1}^{m_j} K(\text{anc}_{t_j-\epsilon}(d_{j,i})) \phi_{d_{j,i}} \right) \\
&\quad + |K_{t_j-\epsilon}| \left(1 - \frac{|K_{t_j-\epsilon}| + \sum_{i \in R_{t_j-\epsilon}} K(\text{anc}_{t_j-\epsilon}(i)) W_{t_j-\epsilon}^{t_j+\delta}(i)}{|K_{t_j-\epsilon}|} \right) \overline{\phi_{t_j-\epsilon}} \\
&= \frac{1}{|K_{t_j-\epsilon}| \overline{W_{t_j-\epsilon}^{t_j+\delta}}} \left(\sum_{i=1}^{n_j} K(\text{anc}_{t_j-\epsilon}(r_{j,i})) \phi_{r_{j,i}} - \sum_{i=1}^{m_j} K(\text{anc}_{t_j-\epsilon}(d_{j,i})) \phi_{d_{j,i}} \right) \\
&\quad - \sum_{i \in R_{t_j-\epsilon}} K(\text{anc}_{t_j-\epsilon}(i)) W_{t_j-\epsilon}^{t_j+\delta}(i) \overline{\phi_{t_j-\epsilon}} \\
&= \frac{1}{|K_{t_j-\epsilon}| \overline{W_{t_j-\epsilon}^{t_j+\delta}}} \left(\sum_{i=1}^{n_j} K(\text{anc}_{t_j-\epsilon}(r_{j,i})) \phi_{r_{j,i}} - \sum_{i=1}^{m_j} K(\text{anc}_{t_j-\epsilon}(d_{j,i})) \phi_{d_{j,i}} \right) \\
&\quad - \left(\sum_{i=1}^{n_j} K(\text{anc}_{t_j-\epsilon}(r_{j,i})) - \sum_{i=1}^{m_j} K(\text{anc}_{t_j-\epsilon}(d_{j,i})) \right) \overline{\phi_{t_j-\epsilon}} \\
&= \frac{1}{|K_{t_j-\epsilon}| \overline{W_{t_j-\epsilon}^{t_j+\delta}}} \left(\sum_{i=1}^{n_j} K(\text{anc}_{t_j-\epsilon}(r_{j,i})) (\phi_{r_{j,i}} - \overline{\phi_{t_j-\epsilon}}) + \sum_{i=1}^{m_j} K(\text{anc}_{t_j-\epsilon}(d_{j,i})) (\overline{\phi_{t_j-\epsilon}} - \phi_{d_{j,i}}) \right) \\
&= \sum_{i=1}^{n_j} \frac{K(\text{anc}_{t_j-\epsilon}(r_{j,i})) (\phi_{r_{j,i}} - \overline{\phi_{t_j-\epsilon}})}{|K_{t_j-\epsilon}| \overline{W_{t_j-\epsilon}^{t_j+\delta}}} + \sum_{i=1}^{m_j} \frac{K(\text{anc}_{t_j-\epsilon}(d_{j,i})) (\overline{\phi_{t_j-\epsilon}} - \phi_{d_{j,i}})}{|K_{t_j-\epsilon}| \overline{W_{t_j-\epsilon}^{t_j+\delta}}}
\end{aligned} \tag{F.6}$$

Next, let $k > \frac{b-a}{\epsilon^*}$, as in the proof of equation 6.3. Then for some $(\delta_j)_{j \in U}, (\epsilon_j)_{j \in U}$, the following equation holds.

$$\begin{aligned}
S_a^{b,k}(K) &= \sum_{s=0}^{k-1} S_{a+s(b-a)/k}^{a+(s+1)(b-a)/k}(K) \\
&= \sum_{t_j \in U} S_{t_j-\epsilon_j}^{t_j+\delta_j}(K)
\end{aligned} \tag{F.7}$$

Note that $0 < \epsilon_j < \epsilon^*$ and $0 \leq \delta_j < \epsilon^*$ for all $j \in U$ since the length of the time intervals are smaller than $\frac{k}{b-a} = \epsilon^*$. Also, for $t_j = b \in U$, $\delta_j = 0$. Hence we can now combine our previous two expressions as follows:

$$\begin{aligned} & S_a^{b,k(K)} \\ &= \sum_{t_j \in U} \left(\sum_{i=1}^{n_j} \frac{K(\text{anc}_{t_j-\epsilon_j}(r_{j,i}))(\phi_{r_{j,i}} - \overline{\phi_{t_j-\epsilon_j}})}{|K_{t_j-\epsilon_j}| \overline{W_{t_j-\epsilon_j}^{t_j}}} + \sum_{i=1}^{m_j} \frac{K(\text{anc}_{t_j-\epsilon_j}(d_{j,i}))(\overline{\phi_{t_j-\epsilon_j}} - \phi_{d_{j,i}})}{|K_{t_j-\epsilon_j}| \overline{W_{t_j-\epsilon_j}^{t_j}}} \right) \end{aligned} \quad (\text{F.8})$$

Note, again, that for all $j \in U$, it must be the case that $\epsilon_j < \frac{k}{b-a}$. Therefore, under the condition that left limits in time of weight functions exist, the following expression holds.

$$\begin{aligned} & S_a^{b(K)} \\ &= \sum_{t_j \in U} \lim_{\epsilon_j \downarrow 0} \left(\sum_{i=1}^{n_j} \frac{K(\text{anc}_{t_j-\epsilon_j}(r_{j,i}))(\phi_{r_{j,i}} - \overline{\phi_{t_j-\epsilon_j}})}{|K_{t_j-\epsilon_j}| \overline{W_{t_j-\epsilon_j}^{t_j}}} + \sum_{i=1}^{m_j} \frac{K(\text{anc}_{t_j-\epsilon_j}(d_{j,i}))(\overline{\phi_{t_j-\epsilon_j}} - \phi_{d_{j,i}})}{|K_{t_j-\epsilon_j}| \overline{W_{t_j-\epsilon_j}^{t_j}}} \right) \end{aligned} \quad (\text{F.9})$$

Left limits in time of weight functions do indeed exist, since this is literally one of our requirements for weight functions, as can be seen in definition 8.1. We can write down equation F.9 using different notation as follows.

$$S_a^{b(K)} = \sum_{t_j \in U} \left(\sum_{i=1}^{n_j} \frac{K^-(r_{j,i})(\phi_{r_{j,i}} - \overline{\phi_{t_j}^-})}{|K_{t_j}^-| \overline{W_{t_j}^{t_j}}} + \sum_{i=1}^{m_j} \frac{K^-(d_{j,i})(\overline{\phi_{t_j}^-} - \phi_{d_{j,i}})}{|K_{t_j}^-| \overline{W_{t_j}^{t_j}}} \right) \quad (\text{F.10})$$

Under the notation used in the statement of the theorem, expression 12.4 immediately follows. \square

Proof. (of corollary 12.4) We can first write out the $\overline{W_{t_j}^{t_j}}$ terms as follows.

$$\begin{aligned} \overline{W_{t_j}^{t_j}} &= \frac{1}{|K_{t_j}^-|} \sum_{i \in R_{t_j}^-} K^-(i)(1 + |C_{t_j}^-| - |D_{t_j}^-|) \\ (\text{using equation F.5}) &= \frac{1}{|K_{t_j}^-|} \sum_{i \in R_{t_j}^-} (|K_{t_j}^-| + \sum_{i=1}^{n_j} K^-(r_{j,i}) - \sum_{i=1}^{m_j} K^-(d_{j,i})) \end{aligned} \quad (\text{F.11})$$

Hence, expression F.10 can alternatively be written as expression 12.5. \square

G Proof of theorem 12.9

In this Appendix, we will omit the superscript (K) for readability purposes.

In order to prove this theorem, we will need the following lemma to circumvent the aforementioned problem of having to deal with discrete summations while migration can happen continuously.

Lemma G.1. *Let $x < y$ such that no birth or death event happens in the interval $(x, y]$, and such that $\sum_{i=1}^{N_t} K(i, t) \neq 0$ for all $t \in (x, y]$. Then for all $k > 0$, the following equations hold.*

$$M_x^{k, (y-x)/k} = M_x^y \quad (\text{G.1})$$

$$\kappa_x^{k, (y-x)/k} = 0 \quad (\text{G.2})$$

Proof. If no birth or death event happens in the interval $(x, y]$, it follows that $W_x^y(i) = 1$ for all replicators $i \in R_x$, so $S_x^y = 0$. Also, $\phi_j = \phi_{\text{anc}_x(j)}$ for all replicators $j \in R_y$, so $\mu_x^y = \kappa_x^y = 0$. Then migration must account for the full change in average phenotype:

$$\begin{aligned} M_x^y &= S_x^y + \mu_x^y + M_x^y + \kappa_x^y \\ &= \overline{\phi_y} - \overline{\phi_x} \end{aligned} \quad (\text{G.3})$$

If no birth or death event happens in the interval $(x, y]$, then the same is true for any subinterval of $(x, y]$. Hence we have the following result for all $k > 0$.

$$\begin{aligned}
M_x^{k,(y-x)/k} &= \sum_{s=0}^{k-1} M_{x+s}^{x+(s+1)(y-x)/k} \\
&= \sum_{s=0}^{k-1} \overline{\phi_{x+(s+1)(y-x)/k}} - \overline{\phi_{x+s(y-x)/k}} \\
&= \overline{\phi_{x+(k-1+1)(y-x)/k}} - \overline{\phi_x} \\
&= \overline{\phi_y} - \overline{\phi_x} \\
&= M_x^y
\end{aligned} \tag{G.4}$$

The following result follows immediately too.

$$\kappa_x^{k,y/k} = 0 \tag{G.5}$$

□

Our strategy for the proof of theorem 12.9 is as follows. We will choose k big enough so that no two elements of U will fall within the same time interval in the form $(a + s(b-a)/k, a + (s+1)(b-a)/k]$. Then for every element of U we will have a unique time interval containing this element. Also, between every two consecutive elements of U we will have a collection of time intervals that, according to lemma G.1, can be described with one single term. Letting k go to infinity will then not increase the number of terms any further.

Proof. (of theorem 12.9) Let

$$\epsilon^* \equiv \min\{|t_i - t_j| \mid t_i, t_j \in U, t_i \neq t_j\} \tag{G.6}$$

as in equation A.1. Let

$$k > \frac{b-a}{\epsilon^*} \tag{G.7}$$

as we have seen in previous proofs as well. In order to avoid clutter, we will use the following definition.

Definition G.2. Let k be given. For all $s \in \{0, 1, \dots, k-1\}$, we write the following.

$$\tau_s \equiv a + s(b-a)/k \tag{G.8}$$

This definition is purely used as shorthand notation to make our equations easier to read. Any time we use it, it will be clear what k is.

By filling in G.2, it can be readily seen that for a property P (where $P = M$ or $P = \kappa$), the following holds.

$$M_a^{b,k} = \sum_{s=0}^{k-1} M_{\tau_s}^{\tau_{s+1}} \tag{G.9}$$

As such, the $(\tau_s, \tau_{s+1}]_{s \in \{0, 1, \dots, k-1\}}$ form a partition of $(a, b]$. As a consequence, since $U \subset (a, b]$, for all $t_j \in U$ there exists a unique $s_j \in \{0, 1, \dots, k-1\}$ such that $t_j \in (\tau_{s_j}, \tau_{s_j+1}]$. Moreover, for $t_i, t_j \in U, i \neq j, t_i \in (\tau_{s_i}, \tau_{s_i+1}]$ and $t_j \in (\tau_{s_j}, \tau_{s_j+1}]$, we have $\tau_{s_i} \neq \tau_{s_j}$. The reason for this is that if $\tau_{s_i} = \tau_{s_j}$, then $t_i, t_j \in (\tau_{s_i}, \tau_{s_i+1}]$ so

$$|t_i - t_j| < \tau_{s_i+1} - \tau_{s_i} = a + (s_i + 1)(b-a)/k - a - s_i(b-a)/k = (b-a)/k < \epsilon^* \tag{G.10}$$

but by definition of ϵ^* , we must have $|t_i - t_j| \geq \epsilon^*$. Let $\epsilon_j \equiv t_j - \tau_{s_j}$ and let $\delta_j \equiv \tau_{s_j+1} - t_j$. Since $t_j \in (\tau_{s_j}, \tau_{s_j+1}]$, it must be that $t_j > \tau_{s_j}$, and hence $\epsilon_j > 0$.

See figure 5 for an illustration of our definitions and findings so far.

We can now write

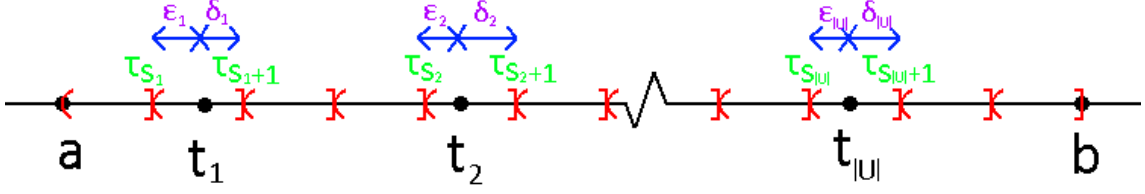


Figure 5: An illustration of our definitions. Note that for any j it can be the case that $\tau_{s_j+1} = t_j$, in which case $\delta_j = 0$. Note also that it may be the case that $b \in U$, though this is chosen to not be so in this specific illustration.

$$\begin{aligned}
M_a^{b,k} &= \sum_{s=0}^{k-1} M_{\tau_s}^{\tau_{s+1}} \\
&= \sum_{s=0}^{k(t_1 - \epsilon_1 - a)/(b-a) - 1} M_{\tau_s}^{\tau_{s+1}} + \sum_{t_j \in U, j \neq |U|} (M_{t_j - \epsilon_j}^{t_j + \delta_j} + \sum_{s=k(t_j + \delta_j - a)/(b-a)}^{k(t_{j+1} - \epsilon_{j+1} - a)/(b-a) - 1} M_{\tau_s}^{\tau_{s+1}}) \\
&\quad + M_{t_{|U|} - \epsilon_{|U|}}^{t_{|U|} + \delta_{|U|}} + \sum_{s=k(t_{|U|} + \delta_{|U|} - a)/(b-a)}^{k-1} M_{\tau_s}^{\tau_{s+1}} \\
&= M_a^{k(t_1 - \epsilon_1 - a)/(b-a), (b-a)/k} + \sum_{t_j \in U, j \neq |U|} (M_{t_j - \epsilon_j}^{t_j + \delta_j} + M_{t_j + \delta_j}^{(k(t_{j+1} - \epsilon_{j+1}) - (t_j + \delta_j))/(b-a), (b-a)/k}) \\
&\quad + M_{t_{|U|} - \epsilon_{|U|}}^{t_{|U|} + \delta_{|U|}} + M_{t_{|U|} + \delta_{|U|}}^{(k(b - (t_{|U|} + \delta_{|U|})))/(b-a), (b-a)/k} \\
(\text{by lemma G.1}) &= M_a^{t_1 - \epsilon_1} + \sum_{t_j \in U, j \neq |U|} (M_{t_j - \epsilon_j}^{t_j + \delta_j} + M_{t_j + \delta_j}^{t_{j+1} - \epsilon_{j+1}}) + M_{t_{|U|} - \epsilon_{|U|}}^{t_{|U|} + \delta_{|U|}} + M_{t_{|U|} + \delta_{|U|}}^b \\
&= M_a^{t_1 - \epsilon_1} + M_{t_2 + \delta_2}^{t_3 - \epsilon_3} + \dots + M_{t_{|U|} + \delta_{|U|}}^b + \sum_{t_j \in U} M_{t_j - \epsilon_j}^{t_j + \delta_j}
\end{aligned} \tag{G.11}$$

and

$$\begin{aligned}
\kappa_a^{b,k} &= \sum_{s=0}^{k-1} \kappa_{\tau_s}^{\tau_{s+1}} \\
&= \sum_{s=0}^{k(t_1 - \epsilon_1 - a)/(b-a) - 1} \kappa_{\tau_s}^{\tau_{s+1}} + \sum_{t_j \in U, j \neq |U|} (\kappa_{t_j - \epsilon_j}^{t_j + \delta_j} + \sum_{s=k(t_j + \delta_j - a)/(b-a)}^{k(t_{j+1} - \epsilon_{j+1} - a)/(b-a) - 1} \kappa_{\tau_s}^{\tau_{s+1}}) \\
&\quad + \kappa_{t_{|U|} - \epsilon_{|U|}}^{t_{|U|} + \delta_{|U|}} + \sum_{s=k(t_{|U|} + \delta_{|U|} - a)/(b-a)}^{k-1} \kappa_{\tau_s}^{\tau_{s+1}} \\
(\text{by lemma G.1}) &= \sum_{t_j \in U} \kappa_{t_j - \epsilon_j}^{t_j + \delta_j}
\end{aligned} \tag{G.12}$$

Since the weight functions are all right continuous in time, it holds for properties P (where P could be M or κ) and $t_2 > t_1$ that

$$P_{t_1}^{t_2} = \lim_{\delta \downarrow 0} P_{t_1}^{t_2 + \delta} = \lim_{\delta \downarrow 0} P_{t_1 + \delta}^{t_2} \tag{G.13}$$

Then

$$\begin{aligned}
\mathcal{M}_a^{b,k} &= \lim_{\epsilon \downarrow 0} (M_a^{t_1-\epsilon} + M_{t_1}^{t_2-\epsilon} + \dots + M_{t_{|U|}}^b + \sum_{t_j \in U} M_{t_j-\epsilon}^{t_j}) \\
&= M_a^{t_1-} + M_{t_1}^{t_2-} + \dots + M_{t_{|U|}}^b + \sum_{t_j \in U} M_{t_j-}^{t_j}
\end{aligned} \tag{G.14}$$

and similarly,

$$\begin{aligned}
\mathcal{K}_a^{b,k} &= \lim_{\epsilon \downarrow 0} \sum_{t_j \in U} \kappa_{t_j-\epsilon}^{t_j+\delta} \\
&= \sum_{t_j \in U} \kappa_{t_j-}^{t_j}
\end{aligned} \tag{G.15}$$

□

Remark G.3. We might be tempted to think that e.g.

$$\mathcal{K}_a^{b,k} = \lim_{\epsilon \downarrow 0} \lim_{\delta \downarrow 0} \sum_{t_j \in U} \kappa_{t_j-\epsilon}^{t_j+\delta} \tag{G.16}$$

as well as a similar statement about $\mathcal{M}_a^{b,k}$, without needing to make any assumptions about (right) continuity, but that is not true, as from our definitions follows that for some values of k , we could have $\delta_j = 0$ for some j . We therefore really need to e.g. assume that

$$\lim_{\epsilon \downarrow 0} \lim_{\delta \downarrow 0} \sum_{t_j \in U} \kappa_{t_j-\epsilon}^{t_j+\delta} = \lim_{\epsilon \downarrow 0} \sum_{t_j \in U} \kappa_{t_j-\epsilon}^{t_j} \tag{G.17}$$

i.e., we need right continuity for the proof to work.

H Proof of theorem 13.6

In order to prove this theorem, we will first write out an analogue to lemma 4.2.

Lemma H.1. For $i \in R_a$, let C_i^b be the set of replication events in the lineage of replicator i in the time interval $(a, b]$ and let D_i^b be the set of death events in the lineage of replicator i in the time interval $(a, b]$. Notice that $w_a^b(i) = 1 + |C_i^b| - |D_i^b|$. Let $\phi_{\text{anc}_a(r_i)}$ be the phenotype of the ancestor at time a of a replicator that is born at replication event r_i and let $\phi_{\text{anc}_a(d_j)}$ be the phenotype of the ancestor at time a of a replicator that dies at replication event d_j . Then:

$$S_a^{b(K)} = \frac{\sum_{i=1}^n K(\text{anc}_a(r_i))\phi_{\text{anc}_a(r_i)} - \sum_{j=1}^m K(\text{anc}_a(d_j))\phi_{\text{anc}_a(d_j)}}{|K_a|\overline{W}_a^{b(K)}} + (\overline{W}_a^{b(K)-1} - 1)\overline{\phi}_a^{(K)} \tag{H.1}$$

Proof. We use an intermediate answer from equation 8.11 as a starting point:

$$\begin{aligned}
S_a^{b(K)} &= \frac{\sum_{i \in R_a} K(i)W_a^b((\tau_s)_i)\phi_i}{\sum_{i \in R_a} K(i)W_a^b(i)} - \overline{\phi}_a^{(K)} \\
&= \frac{\sum_{i \in R_a} K(i)(1 + |C_i^b| - |D_i^b|)\phi_i}{|K_a|\overline{W}_a^{b(K)}} - \overline{\phi}_a^{(K)} \\
&= \frac{\sum_{i \in R_a} K(i)(|C_i^b| - |D_i^b|)\phi_i}{|K_a|\overline{W}_a^{b(K)}} + \frac{\sum_{i \in R_a} K(i)\phi_i}{|K_a|\overline{W}_a^{b(K)}} - \overline{\phi}_a^{(K)} \\
&= \frac{\sum_{i \in R_a} K(i)(\sum_{r_i \in C_i^b} 1 - \sum_{r_i \in D_i^b} 1)\phi_i}{|K_a|\overline{W}_a^{b(K)}} + \frac{\sum_{i \in R_a} K(i)\phi_i}{|K_a|} \frac{|K_a|}{|K_a|\overline{W}_a^{b(K)}} - \overline{\phi}_a^{(K)} \\
&= \frac{\sum_{i \in R_a} K(i)(\sum_{r_i \in C_i^b} \phi_{\text{anc}_a(r_i)} - \sum_{r_i \in D_i^b} \phi_{\text{anc}_a(d_j)})}{|K_a|\overline{W}_a^{b(K)}} + \overline{\phi}_a^{(K)} \overline{W}_a^{b(K)-1} - \overline{\phi}_a^{(K)} \\
&= \frac{\sum_{i=1}^n K(\text{anc}_a(r_i))\phi_{\text{anc}_a(r_i)} - \sum_{j=1}^m K(\text{anc}_a(d_j))\phi_{\text{anc}_a(d_j)}}{|K_a|\overline{W}_a^{b(K)}} + (\overline{W}_a^{b(K)-1} - 1)\overline{\phi}_a^{(K)}
\end{aligned} \tag{H.2}$$

□

Remark H.2. Note that if $K \equiv 1$, this expression reduces to

$$\begin{aligned}
S_a^{b(K)} &= \frac{\sum_{i=1}^n \phi_{\text{anc}_a(r_i)} - \sum_{j=1}^m \phi_{\text{anc}_a(d_j)}}{\sum_{i \in R_a} W_a^b(i)} + (\overline{W}_a^{b(K)} - 1) \overline{\phi}_a \\
&= \frac{\sum_{i=1}^n \phi_{\text{anc}_a(r_i)} - \sum_{j=1}^m \phi_{\text{anc}_a(d_j)}}{N_b} + \left(\frac{N_a}{N_b} - 1\right) \overline{\phi}_a \\
&= \frac{1}{N_b} \left(\sum_{i=1}^n \phi_{\text{anc}_a(r_i)} - \sum_{j=1}^m \phi_{\text{anc}_a(d_j)} + (N_a - N_b) \overline{\phi}_a \right)
\end{aligned} \tag{H.3}$$

which equals the result from lemma 4.2.

Proof. (of theorem 13.6) Note that if $a \uparrow b$, then necessarily $\phi_{\text{anc}_a(r_i)} \rightarrow \phi_{r_i}$, $\phi_{\text{anc}_a(d_j)} \rightarrow \phi_{d_j}$ and $K(\text{anc}_a(r_i)) \rightarrow K(r_i)$ for all i , so that lemma H.1 comes down to

$$S_{b-}^{b(K)} = \frac{\sum_{i=1}^{n_b} K(i) \phi_{r_i} - \sum_{j=1}^{m_b} K(r_i) \phi_{d_j}}{|K_b| - \overline{W}_{b-}^{b(K)}} + (\overline{W}_{b-}^{b(K)} - 1) \overline{\phi}_{b-} \tag{H.4}$$

where r_1, r_2, \dots, r_{n_b} and d_1, d_2, \dots, d_{m_b} are the respective replication and death events at time b . Let us now write out the following.

$$\begin{aligned}
\widehat{S}_a^b &= \lim_{k \uparrow \infty} \sum_{s=0}^{k-1} \mathbf{E}_{\mathcal{K}} [S_{\tau_s}^{\tau_{s+1}}(K) | |K_{\tau_s}| \overline{W}_{\tau_s}^{\tau_{s+1}}(K)] \\
&= \lim_{k \uparrow \infty} \sum_{s=0}^{k-1} \frac{\sum_{K \in \mathcal{K}} |K_{\tau_s}| \overline{W}_{\tau_s}^{\tau_{s+1}}(K) S_{\tau_s}^{\tau_{s+1}}(K)}{\sum_{K \in \mathcal{K}} |K_{\tau_s}| \overline{W}_{\tau_s}^{\tau_{s+1}}(K)} \\
&= \lim_{k \uparrow \infty} \sum_{s=0}^{k-1} \frac{\sum_{K \in \mathcal{K}} |K_{\tau_s}| \overline{W}_{\tau_s}^{\tau_{s+1}}(K) S_{\tau_s}^{\tau_{s+1}}(K)}{N_{\tau_{s+1}}} \\
&= \lim_{k \uparrow \infty} \sum_{s=0}^{k-1} \frac{1}{N_{\tau_{s+1}}} \sum_{K \in \mathcal{K}} S_{\tau_s}^{\tau_{s+1}}(K) |K_{\tau_s}| \overline{W}_{\tau_s}^{\tau_{s+1}}(K)
\end{aligned} \tag{H.5}$$

Let U again be the set of times that a birth and/or death occurs in the time interval $(a, b]$, with $U \equiv \{t_1, t_2, \dots, t_{|U|}\}$. Let ϵ^* as in equation A.1 and let $k > \frac{b-a}{\epsilon^*}$. Obviously, $S_{\tau_s}^{\tau_{s+1}}(K)$ can only be nonzero if there exists a $t_l \in U$ for which $\tau_s < t_l \leq \tau_{s+1}$. As we have seen before, with k this large, for every $s < k$ there either exists a unique $t_l \in U$ such that $\tau_s < t_l \leq \tau_{s+1}$, in which case $S_{\tau_s}^{\tau_{s+1}} = S_{t_l-}^{t_l}$, or there does not exist such a t_l at all. In light of this, we can rewrite expression H.5 into the following.

$$\begin{aligned}
&\lim_{k \uparrow \infty} \sum_{s=0}^{k-1} \frac{1}{N_{\tau_{s+1}}} \sum_{K \in \mathcal{K}} S_{\tau_s}^{\tau_{s+1}}(K) |K_{\tau_s}| \overline{W}_{\tau_s}^{\tau_{s+1}}(K) \\
&= \sum_{t_l \in U} \frac{1}{N_{t_l}} \sum_{K \in \mathcal{K}} S_{t_l-}^{t_l}(K) |K_{t_l}| \overline{W}_{t_l-}^{t_l}(K)
\end{aligned} \tag{H.6}$$

With use of our result from equation H.4, we can rewrite this as follows.

$$\begin{aligned}
& \sum_{t_l \in U} \frac{1}{N_{t_l}} \sum_{K \in \mathcal{K}} S_{t_l}^{t_l(K)} |K_{t_l}|^{-\overline{W_{t_l}^{t_l(K)}}} \\
&= \sum_{t_l \in U} \frac{1}{N_{t_l}} \sum_{K \in \mathcal{K}} \left(\frac{\sum_{i=1}^{n_{t_l}} K(r_i) \phi_{r_i} - \sum_{j'=1}^{m_{t_l}} K(r_i) \phi_{d_j}}{|K_{t_l}|^{-\overline{W_{t_l}^{t_l(K)}}}} + (\overline{W_{t_l}^{t_l(K)}} - 1) \overline{\phi_{t_l}^{(K)}} \right) |K_{t_l}|^{-\overline{W_{t_l}^{t_l(K)}}} \\
&= \sum_{t_l \in U} \frac{1}{N_{t_l}} \sum_{K \in \mathcal{K}} \left(\sum_{i=1}^{n_{t_l}} K(r_i) \phi_{r_i} - \sum_{j'=1}^{m_{t_l}} K(r_i) \phi_{d_j} + |K_{t_l}|^{-\overline{\phi_{t_l}^{(K)}}} - \overline{W_{t_l}^{t_l(K)}} |K_{t_l}|^{-\overline{\phi_{t_l}^{(K)}}} \right) \\
&= \sum_{t_l \in U} \frac{1}{N_{t_l}} \left(\sum_{i=1}^{n_{t_l}} \sum_{K \in \mathcal{K}} K(r_i) \phi_{r_i} - \sum_{j'=1}^{m_{t_l}} \sum_{K \in \mathcal{K}} K(r_i) \phi_{d_j} \right. \\
&\quad \left. + \sum_{K \in \mathcal{K}} |K_{t_l}|^{-\overline{\phi_{t_l}^{(K)}}} - \sum_{K \in \mathcal{K}} \overline{W_{t_l}^{t_l(K)}} |K_{t_l}|^{-\overline{\phi_{t_l}^{(K)}}} |K_{t_l}|^{-\overline{\phi_{t_l}^{(K)}}} \right) \\
&= \sum_{t_l \in U} \frac{1}{N_{t_l}} \left(\sum_{i=1}^{n_{t_l}} \phi_{r_i} - \sum_{j'=1}^{m_{t_l}} \phi_{d_j} + \overline{\phi_{t_l}^{(K)}} - \sum_{K \in \mathcal{K}} \overline{W_{t_l}^{t_l(K)}} |K_{t_l}|^{-\overline{\phi_{t_l}^{(K)}}} \right)
\end{aligned} \tag{H.7}$$

Note that for all $x, y, x < y$, we have (where r_1, r_1, \dots, r_n and r_1, r_d, \dots, d_n are the respective reproduction and death events in the time interval (x, y)):

$$\begin{aligned}
\overline{\phi_x} - \sum_{K \in \mathcal{K}} \overline{W_x^y(K)} |g_j|_x \overline{\phi_x^{(K)}} &= \overline{\phi_x} - \sum_{K \in \mathcal{K}} \frac{1}{|g_j|_x} \sum_{i \in R_x} K(i) W_x^y(K)(i) |g_j|_x \overline{\phi_x^{(K)}} \\
&= \overline{\phi_x} - \sum_{K \in \mathcal{K}} \sum_{i \in R_x} K(i) W_x^y(K)(i) \overline{\phi_x^{(K)}} \\
&= \overline{\phi_x} - \sum_{K \in \mathcal{K}} \sum_{i \in R_x} K(i) (1 + |C_i^y| - |D_i^y|) \overline{\phi_x^{(K)}} \\
&= \overline{\phi_x} - \sum_{K \in \mathcal{K}} \left(\sum_{i \in R_x} K(i) + \sum_{i \in R_x} K(i) |C_i^y| - \sum_{i \in R_x} K(i) |D_i^y| \right) \overline{\phi_x^{(K)}} \\
&= \overline{\phi_x} - \sum_{K \in \mathcal{K}} (|K_x| + \sum_{i \in R_x} K(i) |C_i^y| - \sum_{i \in R_x} K(i) |D_i^y|) \overline{\phi_x^{(K)}} \\
&= \overline{\phi_x} - \sum_{K \in \mathcal{K}} |K_x| \overline{\phi_x^{(K)}} - \sum_{K \in \mathcal{K}} \left(\sum_{i \in R_x} K(i) |C_i^y| + \sum_{i \in R_x} K(i) |D_i^y| \right) \overline{\phi_x^{(K)}} \\
&= \overline{\phi_x} - \overline{\phi_x} - \sum_{i=1}^{N_x} \sum_{K \in \mathcal{K}} K(i) |C_i^y| \overline{\phi_x^{(K)}} + \sum_{i=1}^{N_x} \sum_{K \in \mathcal{K}} K(i) |D_i^y| \overline{\phi_x^{(K)}} \\
&= - \sum_{i=1}^n \sum_{K \in \mathcal{K}} K(\text{anc}_x(r_i)) \overline{\phi_x^{(K)}} + \sum_{j'=1}^m \sum_{K \in \mathcal{K}} K(\text{anc}_x(d_j)) \overline{\phi_x^{(K)}} \\
&= - \sum_{i=1}^n \frac{\sum_{K \in \mathcal{K}} K(\text{anc}_x(r_i)) \overline{\phi_x^{(K)}}}{\sum_{K \in \mathcal{K}} K(\text{anc}_x(r_i))} + \sum_{j=1}^m \frac{\sum_{K \in \mathcal{K}} K(\text{anc}(d_j, x)) \overline{\phi_x^{(K)}}}{\sum_{K \in \mathcal{K}} K(\text{anc}_x(r_i))} \\
&= - \sum_{i=1}^n \mathbf{E}_{\mathcal{K}}[\overline{\phi_x^{(K)}} | K(\text{anc}_x(r_i))] + \sum_{j=1}^m \mathbf{E}_{\mathcal{K}}[\overline{\phi_x^{(K)}} | K(\text{anc}_x(d_j))]
\end{aligned} \tag{H.8}$$

This means that we can rewrite our expression from equation H.7 as follows.

$$\begin{aligned}
& \sum_{t_i \in U} \frac{1}{N_{t_i}} \left(\sum_{i=1}^{n_{t_i}} \phi_{r_i} - \sum_{j'=1}^{m_{t_i}} \phi_{d_j} + \overline{\phi_{t_i-}} - \sum_{K \in \mathcal{K}} \overline{W_{t_i-}^{(K)}} |K_{t_i}| \overline{\phi_{t_i-}^{(K)}} \right) \\
&= \sum_{t_i \in U} \frac{1}{N_{t_i}} \left(\sum_{i=1}^{n_{t_i}} \phi_{r_i} - \sum_{j'=1}^{m_{t_i}} \phi_{d_j} - \sum_{i=1}^{n_{t_i}} \mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_i-}^{(K)}} | K(r_i)] + \sum_{j'=1}^{m_{t_i}} \mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_i-}^{(K)}} | K(d_j)] \right) \\
&= \sum_{t_i \in U} \frac{1}{N_{t_i}} \left(\sum_{i=1}^{n_{t_i}} \phi_{r_i} - \mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_i-}^{(K)}} | K(r_i)] + \sum_{j'=1}^{m_{t_i}} \mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_i-}^{(K)}} | K(d_j)] - \phi_{d_j} \right) \\
&= \sum_{t_i \in U} \left(\sum_{i=1}^{n_{t_i}} \frac{\phi_{r_i} - \mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_i-}^{(K)}} | K(r_i)]}{N_{t_i}} + \sum_{j'=1}^{m_{t_i}} \frac{\mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_i-}^{(K)}} | K(d_j)] - \phi_{d_j}}{N_{t_i}} \right) \\
&= \sum_{t_i \in U} \left(\sum_{i=1}^{n_{t_i}} \frac{\phi_{r_i} - \mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_i-}^{(K)}} | K(r_i)]}{N_{t_i}} + \sum_{j'=1}^{m_{t_i}} \frac{\mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_j}^{(K)}} | K(d_j)] - \phi_{d_j}}{N_{t_j}} \right) \\
&= \sum_{i=1}^n \frac{\phi_{r_i} - \mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_i-}^{(K)}} | K(r_i)]}{N_{t_i}} + \sum_{j'=1}^m \frac{\mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_j}^{(K)}} | K(d_j)] - \phi_{d_j}}{N_{t_j}}
\end{aligned} \tag{H.9}$$

In conclusion:

$$\widehat{S}_a^b = \sum_{i=1}^n \frac{\phi_{r_i} - \mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_i-}^{(K)}} | K(r_i)]}{N_{t_i}} + \sum_{j'=1}^m \frac{\mathbf{E}_{\mathcal{K}}[\overline{\phi_{t_j}^{(K)}} | K(d_j)] - \phi_{d_j}}{N_{t_j}} \tag{H.10}$$

□

I Some derivations from section 13.4

I.1 Calculation for example 9

For ϵ, δ sufficiently small we have

$$\Phi_{t_1-\epsilon}^{t_2+\delta}(g_1) = 2 \tag{I.1}$$

since group g_1 halved in size due to the migration event at time t_1 . Hence, according to lemma E.6,

$$\begin{aligned}
\widehat{M}_{t_1-\epsilon}^{t_2+\delta} &= \mathbf{E}_b(\phi_{b_i} \sum_{j=1}^2 K_{g_j}(\text{anc}(b_i, t_1 - \epsilon)) \Phi_{t_1-\epsilon}^{t_2+\delta}(g_j)) - \overline{\phi_b} \\
&= \frac{1}{3} \sum_{i=1}^3 \phi_{b_i} \sum_{j=1}^2 K_{g_j}(\text{anc}(b_i, t_1 - \epsilon)) \Phi_{t_1-\epsilon}^{t_2+\delta}(g_j) - \frac{1}{3} \\
(\text{since } \phi_1 = \phi_2 = 0) &= \frac{1}{3} \sum_{j=1}^2 K_{g_j}(\text{anc}(b_3, t_1 - \epsilon)) \Phi_{t_1-\epsilon}^{t_2+\delta}(g_j) - \frac{1}{3} \\
(\text{since } K_{g_2}(\phi_{\text{anc}(b_3, t_1 - \epsilon)}) = 0) &= \frac{1}{3} K_{g_1}(\text{anc}(b_3, t_1 - \epsilon)) \Phi_{t_1-\epsilon}^{t_2+\delta}(g_1) - \frac{1}{3} \\
&= \frac{1}{3} \cdot 2 - \frac{1}{3} \\
&= \frac{1}{3}
\end{aligned} \tag{I.2}$$

But because of symmetry, we also have for ϵ', δ' sufficiently small

$$\widehat{M}_{t_2-\epsilon'}^{t_2+\delta'} = \frac{1}{3} \tag{I.3}$$

As such,

$$\widehat{M}_a^b = \frac{2}{3} \neq 0 = \widehat{M}_a^a \tag{I.4}$$

I.2 Proof of theorem 13.11

We first need to introduce a lemma.

Lemma I.1. *Let $x < y$ such that no birth or death event happens in the interval $(x, y]$. Then for all $k > 0$*

$$\widehat{\kappa}_x^{k, (y-x)/k} = 0 \quad (\text{I.5})$$

Proof. (of lemma I.1) If no birth or death event happens in the interval $(x, y]$, then no imperfect transmission happens, either, so all the $\kappa_x^{y(K)}$ are equal to 0. As such, it follows that

$$\widehat{\kappa}_x^{k, (y-x)/k} = 0 \quad (\text{I.6})$$

□

With this lemma, we are equipped to prove theorem 13.11. The proof is very much analogous to the proof of theorem 12.9, and as such, we will not pay too much attention to details.

Proof. (of theorem 12.9) Let ϵ^* , k and τ_s be defined as in equations G.6, G.7 and definition G.2, respectively. Then for the same reasons as outlined in the proof of equation 12.9, for all $t_j \in U$ there exists a unique $s_j \in \{0, 1, \dots, k-1\}$ such that $t_j \in (\tau_{s_j}, \tau_{s_j+1}]$; and for $t_i, t_j \in U$, $i \neq j$, $t_i \in (\tau_{s_i}, \tau_{s_i+1}]$ and $t_j \in (\tau_{s_j}, \tau_{s_j+1}]$, we have $\tau_{s_i} \neq \tau_{s_j}$. Let $\epsilon_j \equiv t_j - \tau_{s_j}$ and let $\delta_j \equiv \tau_{s_j+1} - t_j$. Directly analogous to equation G.12, we have

$$\begin{aligned} \widehat{\kappa}_a^{b, k} &= \sum_{s=0}^{k-1} \widehat{\kappa}_{\tau_s}^{\tau_{s+1}} \\ &= \sum_{s=0}^{k(t_1 - \epsilon_1 - a)/(b-a) - 1} \widehat{\kappa}_{\tau_s}^{\tau_{s+1}} + \sum_{t_j \in U, j \neq |U|} (\widehat{\kappa}_{t_j - \epsilon_j}^{t_j + \delta_j} + \sum_{s=k(t_j + \delta_j - a)/(b-a)}^{k(t_{j+1} - \epsilon_{j+1} - a)/(b-a) - 1} \widehat{\kappa}_{\tau_s}^{\tau_{s+1}}) \\ &\quad + \widehat{\kappa}_{t_{|U|} - \epsilon_{|U|}}^{t_{|U|} + \delta_{|U|}} + \sum_{s=k(t_{|U|} + \delta_{|U|} - a)/(b-a)}^{k-1} \widehat{\kappa}_{\tau_s}^{\tau_{s+1}} \\ (\text{by lemma I.1}) &= \sum_{t_j \in U} \widehat{\kappa}_{t_j - \epsilon_j}^{t_j + \delta_j} \end{aligned} \quad (\text{I.7})$$

Because the weight functions are right continuous in time,

$$\begin{aligned} \widehat{\mathcal{U}}_a^b &= \lim_{\epsilon \downarrow 0} \sum_{t_j \in U} \widehat{\kappa}_{t_j - \epsilon}^{t_j} \\ &= \sum_{t_j \in U} \widehat{\kappa}_{t_j^-}^{t_j} \end{aligned} \quad (\text{I.8})$$

□

J Bibliography

- [1] (Paper) PRICE, G. R. (1970) «Selection and covariance». *Nature*, 227, 520-521
- [2] (Paper) PRICE, G. R. (1972) «Extension of covariance selection mathematics». *Annals of Human Genetics*, 35, 485-490
- [3] (Paper) LEVIN, B. R., BULL, J. J. (1994) «Short-sighted evolution and the virulence of pathogenic microorganisms». *Trends in Microbiology*, 2, 76-81
- [4] (Paper) NOWAK, M. A., MAY, R. M. (1992) «Evolutionary games and spatial chaos». *Nature* 359, 826-829.
- [5] (Paper) HEISLER, I. L., DAMUTH, J. (1987) «A method for analyzing selection in hierarchically structured populations». *The American Naturalist*, 130, 582-602
- [6] (Book) OKASHA, S. (2006) «Evolution and the levels of selection». *Oxford University Press*
- [7] (Thesis, unpublished) VAN SCHIJNDEL, L. L. M.. (2020) «Quantifying multiscale selection: two approaches». *Utrecht University*