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# The evolution of a population under recombination: how to linearise the dynamics

## Kevin J. Dawson[*]

*Plant and Invertebrate Ecology Division, IACR Rothamsted, Harpenden, Herts AL5 2JQ, UK*

**Abstract**

A system of recursions is derived for the dynamics of an infinitely large population, evolving under a very general process of recombination, whereby an individual can inherit genes from an arbitrary number of parents, sampled independently from the population in the proceeding generation. In general, the number of parents sampled is itself a random variable. A procedure is presented for linearising this system of recursions. This generalises the linearisation procedure introduced by Bennett, for the dynamics of an infinite population where offspring are the product of two parents sampled independently from the population. © 2002 Elsevier Science Inc. All rights reserved.

## 1. Introduction

Most animals and plants have life cycles which alternate between haploid (carrying a single copy of every gene) and diploid (carrying two copies of every gene) phases. This alternation is a consequence of sexual reproduction. Haploid cells called *gametes* (sperm and egg cells) unite in pairs to form diploid cells called *zygotes*, which can then proliferate to produce individuals composed of many diploid cells. Diploid cells can undergo a process called *meiosis*, in which the diploid cell divides

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* Tel.: +44-1582-763133x2281; fax: +44-1582-760981.

  *E-mail address:* kevin.dawson@bbsrc.ac.uk (K.J. Dawson).

to produce haploid cells. In general, when a diploid cell (derived from the fusion of two haploid gametes, labelled 1 and 2) undergoes meiosis, each haploid product of meiosis will carry some genes which are inherited from gamete 1, and some from gamete 2. Such a process, where an individual, or cell, inherits genes from more than one parental individual, or cell, is called *recombination*.

So, population geneticists are interested in the dynamics of the composition of a population having a life cycle where union of gametes is followed by meiosis and recombination. A classical problem in population genetics has been to solve the dynamics of the genotype composition of a population, under the following assumptions: (1) the population is *infinitely large*; (2) pairs of gametes unite *at random* (the two gametes in a pair are sampled independently from the population); (3) generations are *discrete* and *non-overlapping*. To be more precise, the problem is to find an explicit solution for the genotypic composition of the population after *t* generations. This problem has been solved. A brief history is given below. For a more detailed history, see [9].

Real populations are obviously *finite* in size, and population geneticists are ultimately more interested in the dynamics of finite populations. The most natural models for finite populations are Markov chains. The analysis of Markov chain models of finite populations incorporating recombination has proved to be extremely challenging, although important results have been obtained in the case of two loci [24,27]. In view of these difficulties, the obvious place to begin with is the limit where the population size tends to infinity. In this large population limit, chance events have a negligible effect on genotype composition over the short term. (The number of generations which it takes for chance events to appreciably change the genotype composition of a population is of the same order as the population size. See for example [18, pp. 24–28].) So, in the short term at least, the evolution of an infinitely large population is essentially deterministic. There are many situations in which population geneticists are interested in short term dynamics of large populations. For example, when previously isolated populations meet and hybridise [7]; and the response when strong selection is applied to a large population, and the response when strong selection is relaxed [13].

While the assumption that pairs of gametes unite *at random*, as described above, is clearly an idealisation, it is believed to be an adequate approximation to the behaviour of many large outcrossing populations. The assumption that generations are *discrete* and *non-overlapping* applies to many species, including annual plants and many insects. However, the principal justification for this assumption is that this is the simplest case. Age structure leads to an enlarged system of recursions.

We follow the genotype composition in the haploid phase at each generation (rather than the diploid phase), because the resulting dynamics are simpler. Furthermore, the genotype composition of the population of diploid zygotes is completely determined by the population of haploid gametes from which they are formed.

Progress with this problem began when Robbins [23] linearised, and hence solved, the dynamics of an infinitely large population with two arbitrarily linked, diallelic

loci. Geiringer [12] showed how to solve the analogous problem for three arbitrarily linked loci. Geiringer [11] demonstrated that for an arbitrary number of loci, it is always possible to linearise the dynamics. However, her linearisation procedure was rather cumbersome.

Bennett [3], building on the work of Geiringer [11], indicated an elegant general solution to the dynamics of an infinitely large population under meiosis and random union of gametes—linearising, and simultaneously diagonalising, the dynamics. Bennett [3] found a recursive method for defining a set of variables (or "principal components" as he called them) consisting of the allele frequencies (which are invariant under meiosis and union of gametes), together with quantities which measure departures from linkage equilibrium, and which decay geometrically at rates determined by the recombination rates. However, Bennett nowhere stated his recursive algorithm explicitly, nor did he give a general formula for his measures of linkage disequilibrium, for an arbitrary number of loci.

Dawson [9] presented a method for obtaining explicit expressions for Bennett's variables in terms of the "allelic moments" (introduced by Geiringer [11]). It was established that the transformation from the allelic moments to Bennett's variables, and the inverse transformation, always have the form that Bennett claimed. Recursions for calculating the coefficients in the forward transformation and the coefficients in the inverse transformation were derived. In general, these coefficients can be expressed as rational functions of the probabilities of the different recombination events.

In certain special cases, explicit expressions are available for Bennett's variables for arbitrary numbers of loci. For example, when the haploid offspring of a pair of haploid parents has probability 1/2 of receiving its allele at any given locus for either parent, and where the transmission of alleles to the offspring occurs independently at all loci—a situation referred to as "unlinked loci". Turelli and Barton [26] recognised that in this case, Bennett's variables can be equated with a certain set of multivariate cumulants. Explicit formulae are available for the multivariate cumulants [25, pp. 437–438]. In the forthcoming paper [10] I generalise this result, and present an alternative derivation.

Baake [2] analysed the dynamics of a population evolving under random union of gametes and recombination, in the special case where loci are arranged in a sequence (corresponding to a linear chromosome), and following the union of two haploid gametes, recombination occurs by no more than one "cross-over". This is a reasonable assumption for a set of loci which lie close together on the same chromosome. Interestingly, this turns out to be a "singular case", where Bennett's variables are not uniquely defined. Here there are many different sets of variables which decay geometrically under random union of gametes and recombination. Baake [2] obtained expressions for a set of variables which decay in this way. Remarkably, the coefficients in the transformation from the factorial moments to these variables (and its inverse) are purely combinatorial, and independent of the recombination probabilities. Baake [2] also considered the dynamics when mutation is present.

Alternative representations of the solution for the dynamics of an infinitely large population under random union of gametes and recombination have been obtained using genetic algebras. See in particular [14,15,19,20,22]. For useful reviews of this literature, see [16,17].

Using genetic algebras (in particular, the differential operator approach introduced by Reiersol [22]), Lyubich [19] derived expressions for Bennett's variables in terms of certain measures of linkage disequilibrium. However, the expressions are not the same as those found by Bennett. (They do not express Bennett's variables in terms of the allelic moments.) This work is also covered in [20, Chapter 6].

It is possible to write down recursions for the dynamics of a population where offspring are produced from their parents by a more general process of recombination, where an individual can receive its genes from an arbitrary number of parents, sampled at random from the previous generation. These recursions include as a special case, the more familiar recursions for the genetic composition of a population with a standard life cycle where reproduction is bi-parental, with random pairing of gametes followed by meiosis.

More general processes of recombination involving $d > 2$ parents are almost unknown in nature. (Recombination events of this type may occur sporadically among certain viruses. For example, the segmented double-stranded RNA viruses: reoviruses, rotaviruses and influenza viruses.) However, exotic processes of recombination can be incorporated into artificial evolutionary systems. For a review of recombination processes which have been used for bi-parental reproduction in genetic algorithms, see [21].

There is one other context where recombination processes involving multiple parents may play a role. Individuals in a human population may inherit culturally transmitted traits form many individuals, or "cultural parents". For example, linguistic traits such as vocabulary, pronunciation and syntax are typically influenced by many individuals. For simple models of cultural transmission, see [5,6]; and in particular, the multifactor model introduced by Boyd and Richardson [5, pp. 76–79]. See also [8]. The more general process of recombination introduced below may serve as rather crude models of cultural inheritance in humans and some other species [28].

## 2. Allele types and genotypes

In this section, I define the space of genotypes, and at the same time, introduce some useful population genetic terminology.

In population genetics, the term *locus* is used to specify the discrete elements between which recombination can occur. Provided that recombination events are much more common between genes than within genes, it is appropriate to identify genes with loci. A particular gene in a particular individual can be referred to as an *allele copy*. The alternative types of a particular gene coexisting within a population are referred to as *allele types*. Here, we assume that all loci are diallelic. That

is, only two allele types are present in the population. These are arbitrarily labelled 0, 1.

Let $S$ denote a set of $n$ loci, labelled $1, 2, \ldots, n$. So $S = \{1, 2, \ldots, n\}$. A haploid individual carries one copy of each locus, each of which is occupied by an allele copy which has a particular allele type. This ordered sequence of allele types is the *genotype* of the haploid individual. In the diallelic case, the $2^n$ distinct genotypes can be put into a one-to-one correspondence with the $2^n$ sub-sets of $S$. The genotype corresponding to set $U \subset S$ is the genotype where all loci belonging to set $U$ are occupied by alleles of type 1, and all loci belonging to $S - U$ (the complement of $U$ in $S$) are occupied by alleles of type 0.

## 3. Partitions of sets

Before introducing the terminology for the process of recombination, it will be helpful to first introduce some notation and terminology for partitions of sets. A *partition* $\Theta$ of a set $S$ is a set of non-empty disjoint sub-sets of $S$, the union of which is the set $S$ itself. (That is $\bigcup_{A \in \Theta} A = S$.) Let $\pi(S)$ denote the set of all distinct partitions of a set $S$.

A partition $\Theta$ is said to be *finer* than a partition $\Psi$, whenever $\Theta$ and $\Psi$ are both partitions of the same set, and $\Theta$ can be obtained from $\Psi$ by: (i) replacing each element of $\Psi$ by a partition of that element; and then (ii) forming the union of all these partitions. This relationship is denoted by $\Theta \prec \Psi$. We can also express this relationship by saying that the partition $\Theta$ is a *refinement* of the partition $\Psi$. Alternatively, we can say that $\Psi$ is coarser than $\Theta$ (which can also be denoted by $\Psi \succ \Theta$). This terminology and notation is conventional. See for example Aigner [1, pp. 12–13]. (However, in Aigner's notation, the symbol $\prec$ is underscored to emphasise that $\Theta \prec \Psi$ includes the case where $\Theta = \Psi$.) Notice that $\Theta \prec \Psi$ implies $|\Psi| \leqslant |\Theta|$.

Unfortunately, in a previous paper [9], I used the unconventional notation $\Psi \lhd \Theta$, in place of $\Psi \succ \Theta$.

I will now introduce some more notation which is not conventional. A partition $\Theta$ of a set $S$ *induces* a partition on every sub-set of $S$. There is a partition $\Phi$ of $U \subset S$, which has the property that: for every element $A \in \Theta$, either $A \cap U = \emptyset$ or $A \cap U \in \Phi$. We will say that the partition $\Theta$ of $S$ *induces* the partition $\Phi$ of $U$. This relationship will be expressed by the notation $\Phi = \Theta \overset{\Rightarrow}{\cap} U$. This notation will simplify the presentation of the recursions in Section 7.

For a pair of partitions $\Theta, \Phi$, we will say that $\Theta$ *induces* $\Phi$ if there exists any set $U$ such that $\Phi = \Theta \overset{\Rightarrow}{\cap} U$. This relationship will be expressed by the notation $\Theta \Rightarrow \Phi$.

Notice that if $\Theta \prec \Psi$, then $\Theta$ can be expressed as the union of certain partitions (the $\Theta \overset{\Rightarrow}{\cap} U$) of the elements of $\Psi$ (the $U \subset \Psi$). In symbols, we have

$$\bigcup_{U \in \Psi} \left( \Theta \overset{\rightrightarrows}{\cap} U \right) = \Theta \quad \text{for } \Psi : \Theta \prec \Psi. \tag{3.1}$$

In a previous paper [9] I introduced the closely related notation $U \overset{\rightarrow}{\cap} \Theta$, for the relationship which can now be defined as

$$U \overset{\rightarrow}{\cap} \Theta = \begin{cases} \Theta \overset{\rightrightarrows}{\cap} U & \text{if } \left( \Theta \overset{\rightrightarrows}{\cap} U \right) \subset \Theta, \\ \emptyset & \text{otherwise.} \end{cases}$$

The earlier notation $U \overset{\rightarrow}{\cap} \Theta$ is now redundant, and will not be used in what follows.

Lyubich [19, p. 85] used the terminology "$\Theta$ is an *extension* of $\Phi$", in place of "$\Theta$ *induces* $\Phi$". (Lyubich [19, p. 87] also used the terminology "$\Phi$ is the *restriction* to $U \subset S$ of $\Theta$".) Unfortunately Lyubich [19] used the notation $\Theta \succ \Phi$ in place of $\Theta \Rightarrow \Phi$. What is more, Lyubich [20, pp. 235–236] retained the notation $\Theta \succ \Phi$, but used the terminology "$\Phi$ *refines* $\Theta$", along with "the partition $\Theta$ of $S$ induces the partition $\Phi$ of $U$". Lyubich's [20] use of the term "refine" must not be confused with the more conventional use of that term (as for example by Aigner [1]).

Closely related to the concept of a partition is what I will call an *ordered partition*. An ordered partition of a set $S$ is an ordered sequence $(S_1, S_2, \ldots, S_d)$ of disjoint sub-sets of $S$, the union of which is the set $S$ itself (that is $\bigcup_{a=1}^{d} S_a = S$). Any number of empty sets may be included in the sequence $(S_1, S_2, \ldots, S_d)$ (since empty sets are disjoint in the sense that $A \cap \emptyset = \emptyset$ for any set $A$).

Every *ordered partition* of a set induces a *partition* of the same set. Let *unordered* $(U_1, U_2, \ldots, U_d)$ denote the partition induced by the ordered partition $(U_1, U_2, \ldots, U_d)$. This is the partition

$$unordered\,(U_1, U_2, \ldots, U_d) = \left\{ A : A \in \{U_1, U_2, \ldots, U_d\}, A \neq \emptyset \right\}. \tag{3.2}$$

## 4. The recombinational distribution

The very general recombination process under consideration here is as follows. First, $d$ (the sample size) is chosen from a probability distribution $\{\gamma_d\}$ on the positive integers $1, 2, \ldots$ Then $d$ individuals are chosen independently from the population. These $d$ individuals, labelled $1, 2, \ldots, d$, play the part of "parents" in the generalised recombination process. So, $\gamma_d$ is the probability that the number of parents is $d$. The genotype of the offspring is constructed from the genotypes of the parents as follows. For each locus $i \in S$, a parent $P(i)$ is chosen at random from among the parents $1, 2, \ldots, d$. $P(i)$ is the "parent of origin" for the allele copy at locus $i$ in the offspring. The joint distribution of $P(1), P(2), \ldots, P(n)$ will be referred to as the *ordered recombinational distribution*.

The possible outcomes of $P(1), P(2), \ldots, P(n)$ will be referred to as *ordered recombination events*. Every ordered recombination event can be represented as an

*ordered partition* $(S_1, S_2, \ldots, S_d)$ of the set of loci $S$, where $S_i$ is the set of loci that an individual received from parent $i$.

Let $r_d(U_1, U_2, \ldots, U_d)$ denote the probability that an individual receives its alleles at the loci belonging to $U_1$ from parent 1, its alleles at the loci belonging to $U_2$ from parent 2, $\ldots$, and its alleles at the loci belonging to $U_d$ from parent $d$, given that there are exactly $d$ parents. It follows from this definition that these probabilities must satisfy the identity

$$\sum_{\substack{(U_1, U_2, \ldots, U_d): \bigcup_{a=1}^{d} U_a = U \\ U_a \cap U_b = \emptyset \quad \text{for } a \neq b \\ A_1 \subset U_1, \ldots, A_d \subset U_d}} r_d(U_1, U_2, \ldots, U_d) = r_d(A_1, A_2, \ldots, A_d), \qquad (4.1)$$

for any given ordered partition $(A_1, A_2, \ldots, A_d)$, and any set $U$ satisfying $(\bigcup_{a=1}^{d} A_a) \subset U \subset S$.

In view of this relationship, it is natural to define $r_d(\emptyset, \emptyset, \ldots, \emptyset) = 1$ so that the obvious identity

$$\sum_{\substack{(U_1, U_2, \ldots, U_d): \bigcup_{a=1}^{d} U_a = U \\ U_a \cap U_b = \emptyset \quad \text{for } a \neq b}} r_d(U_1, U_2, \ldots, U_d) = 1$$

is a special case of (4.1).

The ordered recombination event specified by the ordered partition is specific to a particular labelling of the parents. We can also define *unordered recombination events*, which take no account of the how parents are labelled, and depend only on the partition which is induced on the set of loci $S$. The corresponding *recombinational distribution* is a probability distribution on $\pi(S)$.

Let $r_d(\Theta)$ denote the probability that the unordered recombination event induces a partition $\Theta$ on the set of loci $U \subset S$, given that there are exactly $d$ parents. That is

$$r_d(\Theta) = \sum_{(U_1, U_2, \ldots, U_d): unordered(U_1, U_2, \ldots, U_d) = \Theta} r_d(U_1, U_2, \ldots, U_d), \qquad (4.2)$$

where the number of terms in this summation is $d!/(d - |\Theta|)!$.

It follows directly from definition (4.2) (and also via the identity (4.1)) that the $r_d(\Theta)$ must satisfy the identity

$$\sum_{\substack{\Theta: \Theta \in \pi(U) \\ \Theta \Rightarrow \Phi}} r_d(\Theta) = r_d(\Phi) \qquad (4.3)$$

for any set $U$ satisfying $\bigcup_{B \in \Phi} B \subset U \subset S$. So, it is natural to define $r_d(\{\emptyset\}) = 1$ to make the obvious identity

$$\sum_{\Theta: \Theta \in \pi(U)} r_d(\Theta) = 1,$$

a special case of (4.3).

A set containing on a single element $\{i\}$ has only one possible partition $\{\{i\}\}$. Therefore

$$r_d(\{\{i\}\}) = 1 \quad \text{for every } i \in S. \tag{4.4}$$

Let $r(\Theta)$ denote the probability that the unordered recombination event induces a partition $\Theta$ on the set of loci $U \subset S$. That is

$$r(\Theta) = \sum_{d=|\Theta|}^{\infty} \gamma_d r_d(\Theta). \tag{4.5}$$

It follows directly from definition (4.5) (and also via the identity (4.3)) that the $r(\Theta)$ must satisfy the identity

$$\sum_{\substack{\Theta : \Theta \in \pi(U) \\ \Theta \Rightarrow \Phi}} r(\Theta) = r(\Phi) \tag{4.6}$$

for any set $U$ satisfying $\bigcup_{B \in \Phi} B \subset U \subset S$. So, it is natural to define $r(\{\emptyset\}) = 1$ to make

$$\sum_{\Theta : \Theta \in \pi(U)} r(\Theta) = 1,$$

a special case of (4.6). Also, notice that

$$r(\{\{i\}\}) = 1 \quad \text{for every } i \in S. \tag{4.7}$$

## 5. The recursions for the genotype frequencies

For each $U \subset S$, let $g_t(U \,|\, S)$ denote the frequency, in the population at generation $t$, of the genotype where all loci belonging to set $U$ are occupied by alleles of type 1:

$$\sum_{U : U \subset S} g_t(U \,|\, S) = 1. \tag{5.1}$$

Suppose that an individual had exactly $d$ parents, and that it received its alleles at all loci belonging to the set $R_a$, from parent $a$ (for $a = 1, 2, \ldots, d$). Further suppose that parent $a$ carries alleles of type 1 at all loci belonging to the set $A_a$, and allele 0 at the loci belonging to $S - A_a$ (for $a = 1, 2, \ldots, d$). Now, if $U$ is the set of loci at which the individual carries alleles of type 1 (so that $S - U$ is the set of loci at which the offspring carries alleles of type 0), then these sets must satisfy the following conditions:

$$U \subset S \quad \text{and} \quad A_a \subset S \text{ for } a = 1, 2, \ldots, d, \tag{5.2a}$$

$$\bigcup_{a=1}^{d} R_a = S, \tag{5.2b}$$

$$R_a \cap R_b = \emptyset \quad \text{for } a \neq b, \tag{5.2c}$$

$$\bigcup_{a=1}^{d} (R_a \cap A_a) = U. \tag{5.2d}$$

So, we can write down the recursion

$$g_{t+1}(U|S) = \sum_{d=1}^{\infty} \gamma_d \left( \sum_{\substack{(R_1, R_2, \dots, R_d): \bigcup_{a=1}^{d} R_a = S \\ R_a \cap R_b = \emptyset \quad \text{for } a \neq b}} \right.$$

$$\left. \sum_{\substack{(A_1, A_2, \dots, A_d): A_1, \dots, A_d \subset S \\ \bigcup_{a=1}^{d} (R_a \cap A_a) = U}} r_d(R_1, R_2, \dots, R_d) \left( \prod_{a=1}^{d} g_t(A_a|S) \right) \right)$$

$$= \sum_{d=1}^{\infty} \gamma_d \left( \sum_{\substack{(R_1, R_2, \dots, R_d): \bigcup_{a=1}^{d} R_a = S \\ R_a \cap R_b = \emptyset \text{ for } a \neq b}} r_d(R_1, R_2, \dots, R_d) \right.$$

$$\left. \times \left( \sum_{\substack{(A_1, A_2, \dots, A_d): A_1, \dots, A_d \subset S \\ \bigcup_{a=1}^{d} (R_a \cap A_a) = U}} \left( \prod_{a=1}^{d} g_t(A_a|S) \right) \right) \right)$$

$$\text{for } U \subset S. \tag{5.3}$$

The following proposition enables us to rewrite (5.3) in a new form.

**Proposition 1.** *The set of conditions* (5.2) *is equivalent to the following set of conditions:*

$$U \subset S \quad and \quad A_a \subset S \text{ for } a = 1, 2, \dots, d, \tag{5.4a}$$

$$\bigcup_{a=1}^{d} R_a = S, \tag{5.4b}$$

$$R_a \cap R_b = \emptyset \quad for \ a \neq b, \tag{5.4c}$$

$$R_a \cap U = R_a \cap A_a \quad for \ a = 1, 2, \dots, d. \tag{5.4d}$$

For a proof of Proposition 1, see Appendix A. By using Proposition 1, we can rewrite (5.3) in the form

$$g_{t+1}(U|S) = \sum_{d=1}^{\infty} \gamma_d \left( \sum_{\substack{(R_1, R_2, \ldots, R_d): \bigcup_{a=1}^d R_a = S \\ R_a \cap R_b = \emptyset \quad \text{for } a \neq b}} r_d(R_1, R_2, \ldots, R_d) \right.$$

$$\left. \times \left( \sum_{A_1 : R_1 \cap U = R_1 \cap A_1} \cdots \sum_{A_d : R_d \cap U = R_d \cap A_d} \left( \prod_{a=1}^d g_t(A_a | S) \right) \right) \right)$$

$$= \sum_{d=1}^{\infty} \gamma_d \left( \sum_{\substack{(R_1, R_2, \ldots, R_d): \bigcup_{a=1}^d R_a = S \\ R_a \cap R_b = \emptyset \quad \text{for } a \neq b}} r_d(R_1, R_2, \ldots, R_d) \right.$$

$$\left. \times \left( \prod_{a=1}^d \left( \sum_{A_a : R_a \cap U = R_a \cap A_a} g_t(A_a | S) \right) \right) \right)$$

$$= \sum_{d=1}^{\infty} \gamma_d \left( \sum_{\substack{\Theta : \Theta \in \pi(S) \\ |\Theta| = d}} r_d(\Theta) \left( \prod_{R \in \Theta} \left( \sum_{A : R \cap U = R \cap A} g_t(A|S) \right) \right) \right)$$

$$\text{for } U \subset S. \tag{5.5}$$

Using definition (4.5) of $r(\Theta)$, we can rewrite (5.5) in the from

$$g_{t+1}(U|S) = \sum_{\Theta : \Theta \in \pi(S)} r(\Theta) \left( \prod_{R \in \Theta} \left( \sum_{A : R \cap U = R \cap A} g_t(A|S) \right) \right) \quad \text{for } U \subset S. \tag{5.6}$$

## 6. Geiringer's transformation

In the case of bi-parental reproduction, Geiringer [11] found a change of variables that transforms the system of recursions (5.6) (which is quadratic in the special case of bi-parental reproduction) into one which has a particular hierarchical form. A system of recursions of this special form can be linearised, and hence solved [11]. This underlying hierarchical (and hence, linear) structure is not immediately apparent in the original system of recursions. So, Geiringer's transformation to a hierarchical form is the crucial first step in the linearisation of this quadratic system. Geiringer's transformation also transforms the more general system of recursions (5.6) to a hierarchical form. Again, this is the crucial first step in the linearisation of this system.

Let $p_t(U)$ denote the frequency, among the population of gametes in generation $t$, of all those genotype that have the loci belonging to $U$ occupied by 1 alleles. From this definition it follows that

$$p_t(U) = \sum_{A:U \subset A \subset S} g_t(A|S). \tag{6.1}$$

This is the change of variables introduced by Geiringer [11]. It is easy to verify the inverse relationship

$$g_t(U|S) = \sum_{A:U \subset A \subset S} (-1)^{|A-U|} p_t(A) \tag{6.2}$$

by substituting (6.1) into (6.2) and changing the order of summation. (This fact could be established using the general form of the Möbius inversion formula, see for example [4].) Therefore, the variables $p_t(U)$ completely determine the genotype frequencies $g_t(U|S)$.

A very simple relationship exists between the multivariate generating function of the $g_t(U|S)$, and that of the $p_t(U)$. Let

$$G_t(z_1, \ldots, z_n \,|\, S) = \sum_{U:U \subset S} g_t(U|S) \left( \prod_{i \in U} z_i \right), \tag{6.3}$$

and

$$P_t(z_1, \ldots, z_n | S) = \sum_{U:U \subset S} p_t(U) \left( \prod_{i \in U} z_i \right). \tag{6.4}$$

The generating function $G_t(z_1, \ldots, z_n | S)$ is the probability generating function for a set of random variables defined as follows. First, let $\chi_X(i)$ denote the "indicator function" of a set $X$. That is $\chi_X(i) = 1$ when $i \in X$, and $\chi_X(i) = 0$ otherwise. Now suppose that $X_t$ is the set representing the genotype of a haploid individual chosen at random from the population at generation $t$. The random variables $(\chi_{X_t}(1), \ldots, \chi_{X_t}(n))$ are referred to as "allelic indicators". Clearly, $G_t(z_1, \ldots, z_n | S)$ is the generating function for this set of random variables.

It can be shown (by a change in the order of summation) that

$$P_t(z_1, \ldots, z_n | S) = G_t(z_1 + 1, \ldots, z_n + 1 | S). \tag{6.5}$$

This is exactly the general relationship between the probability generating function of a multivariate distribution, and the corresponding multivariate factorial moment generating function (see [25, pp. 83, 102–104]). Therefore, $P_t(z_1, \ldots, z_n | S)$ is the factorial moment generating function of these same random variables. In general, the factorial moments $m_t(k_1, \ldots, k_n)$ are defined by the Taylor expansion

$$P_t(z_1, \ldots, z_n | S) = \sum_{k_1=1}^{\infty} \cdots \sum_{k_n=1}^{\infty} \frac{m_t(k_1, \ldots, k_n)}{k_1! \cdots k_n!} z_1^{k_1} \cdots z_n^{k_n}.$$

Therefore

$$p_t(U) = m_t\big(\chi_U(1), \ldots, \chi_U(n)\big) \quad \text{for } U \subset S, \tag{6.6a}$$

while

$$m_t(k_1, \ldots, k_n) = 0 \quad \text{if any of } k_1, \ldots, k_n \text{ exceeds 1.} \tag{6.6b}$$

The factorial moment (about the origin) $m_t(\chi_U(1), \ldots, \chi_U(n))$ coincides with the corresponding moment (about the origin). However, the higher-order factorial moments $(m_t(k_1, \ldots, k_n))$, where any of $k_1, \ldots, k_n$ exceeds 1) are all zero, and do not coincide with the corresponding moments (see [9]). So, while $P_t(z_1, \ldots, z_n|S)$ is a factorial moment generating function, it is not a moment generating function. For this reason, it may be more appropriate to refer to the $p_t(U)$ as factorial moments.

Previously [9], I referred to the $p_t(U)$ as the "allelic moments", in order to avoid confusion with another set of factorial moments—the "recombinational moments"—also discussed in that paper. Here, as no such confusion can arise, I will simply refer to the $p_t(U)$ as the "factorial moments".

The recursions for the $p_t(U)$ are easily derived from those for the genotype frequencies as follows. From definition (6.1), we see that

$$p_t(S) = g_t(S|S) \tag{6.7}$$

for any set of loci $S$. So, putting $U = S$ in (5.6), we obtain

$$g_{t+1}(S|S) = \sum_{\Theta : \Theta \in \pi(S)} r(\Theta) \left( \prod_{R \in \Theta} \left( \sum_{A : R \subset A \subset S} g_t(A|S) \right) \right). \tag{6.8}$$

Using definition (6.1) we can write this as

$$p_{t+1}(S) = \sum_{\Theta : \Theta \in \pi(S)} r(\Theta) \left( \prod_{R \in \Theta} p_t(R) \right). \tag{6.9}$$

Again, this is true for any set of loci $S$. So, we have

$$p_{t+1}(U) = \sum_{\Theta : \Theta \in \pi(U)} r(\Theta) \left( \prod_{R \in \Theta} p_t(R) \right) \quad \text{for all } U \subset S. \tag{6.10}$$

Note that the "allele frequencies" $p_t(\{i\})$ are invariant: $p_{t+1}(\{i\}) = p_t(\{i\})$.

In the next section, I consider a further change of variables of the type introduced by Bennett [3].

## 7. A generalisation of Bennett's transformation

Bennett [3] found that there exists a set of variables $\{b_t(U)\}$ of the form

$$b_t(U) = \sum_{\Theta \in \pi(U)} C(\Theta) \left( \prod_{A \in \Theta} p_t(A) \right) \tag{7.1}$$

(where the coefficients $C(\Theta)$ are constants, yet to be determined), which satisfy linear recursions of the special (diagonal) form

$$b_{t+1}(U) = \lambda(U)b_t(U) \tag{7.2}$$

(where the $\lambda(U)$ are constants, yet to be determined). Furthermore, Bennett showed that the rate of decay $\lambda(U)$ of the variable $b_t(U)$ is equal to $r(\{U\})$ (the probability of non-recombination across the loci belonging to $U$). Bennett [3] also found that the inverse of this transformation (7.1) is of the form

$$p_t(U) = \sum_{\Theta \in \pi(U)} \bar{C}(\Theta) \left( \prod_{A \in \Theta} b_t(A) \right) \tag{7.3}$$

(where the coefficients $\bar{C}(\Theta)$ are constants, yet to be determined). Notice that the transformation (7.1) and its inverse (7.3) are of essentially the same form (as will be verified below).

Bennett [3] referred to the variables $b_t(U)$ as "principle components". Here (as in [9]), I refer to the $b_t(U)$ as "Bennett's variables". Bennett [3] found a recursive method for constructing the transformation (7.1) from the allelic moments the $p_t(U)$ to his new set of variables $b_t(U)$, and a recursive method for constructing the inverse of this transformation (7.3). (In fact in Bennett's approach, the inverse transformation is derived first.)

Below, I present a recursion (7.11) for calculating the coefficients $C(\Theta)$ given the $r(\Theta)$, and a recursion (7.7) for calculating the coefficients $\bar{C}(\Theta)$ given the $r(\Theta)$. I also present a recursion (7.13) for calculating the coefficients $C(\Theta)$ given the coefficients $\bar{C}(\Theta)$, and a formally identical recursion (7.15) for calculating the coefficients $\bar{C}(\Theta)$ from the coefficients $C(\Theta)$.

The recursive equations for the $C(\Theta)$ are constructed in such a way that the functions defined in (7.1) must have property (7.2). So, if these equations for the $C(\Theta)$ do have a solution, then there must be functions having property (7.2) that are of form (7.1). In fact, below I establish that the recursive equations for the $C(\Theta)$ and for the $\bar{C}(\Theta)$ always have a solution. This confirms that a set of variables satisfying (7.2) always exists, and that the transformation (7.1) and the inverse transformation (7.3) are always of this same form. Furthermore, I show that for given initial conditions, this solution is unique except in certain singular cases.

In order to write these recursions in a compact form, we now make use of the notation introduced in Section 3. The recursion for calculating the coefficients $\bar{C}(\Theta)$, given the $r(\Theta)$, is

$$\left( \left( \prod_{R \in \Theta} \lambda(R) \right) - r(\{U\}) \right) \bar{C}(\Theta) = \sum_{\substack{\Psi : \Theta \prec \Psi \\ \Psi \neq \{U\}}} r(\Psi) \left( \prod_{A \in \Psi} \bar{C}(\Theta \overset{\rightarrow}{\cap} A) \right), \tag{7.4}$$

where $U = \bigcup_{R \in \Theta} R$. For a derivation of this recursion, see Appendix B. The condition $\Theta \prec \Psi$ (defined in Section 3) ensures that the partition $\Psi$ can be generated from the partition $\Theta$, by the following procedure: (i) Represent $\Theta$ as a set of sets. Partition $\Theta$ into non-empty disjoint sub-sets. (ii) Replace each of these sub-sets by the union of all its elements (these elements are themselves sets of loci).

For the trivial partition of a set into one part (a partition $\Theta$ where $|\Theta| = 1$), (7.4) reduces to

$$\big(\lambda(U) - r(\{U\})\big)\bar{C}(\{U\}) = 0. \tag{7.5}$$

Therefore, if $\bar{C}(\{U\}) \neq 0$, then

$$\lambda(U) = r(\{U\}) \tag{7.6}$$

for any set $U \neq \emptyset$. Other than the constraint $\bar{C}(\{U\}) \neq 0$, the value of $\bar{C}(\{U\})$ is arbitrary. So, the values of the $\bar{C}(\Theta)$, where $|\Theta| = 1$, must be specified as initial conditions. For convenience, we can choose $\bar{C}(\{U\}) = 1$ for every set $U \neq \emptyset$. Substituting (7.6) back into (7.4), we obtain the recursion

$$\left(\left(\prod_{R \in \Theta} r(\{R\})\right) - r(\{U\})\right)\bar{C}(\Theta) = \sum_{\substack{\Psi : \Theta \prec \Psi \\ \Psi \neq \{U\}}} r(\Psi)\left(\prod_{A \in \Psi} \bar{C}(\Theta \overset{\rightarrow}{\cap} A)\right). \tag{7.7}$$

From this we can obtain the rest of the $\bar{C}(\Theta)$.

Because of its recursive nature, it is obvious that the system of equations (7.7) always has a unique solution, except in certain "singular" cases. The form of the left-hand side of (7.7) immediately alerts us to the possibility of these singular cases. Any partition $\Theta = \{U_1, U_2, \ldots, U_k\}$ of set of loci $U$, where

$$r(\{U_1\})\, r(\{U_2\}) \cdots r(\{U_k\}) = r(\{U\}),$$

will be referred to as a "singular partition". At a singular partition $\Theta$, the recursion (7.4) reduces to $0$, $\bar{C}(\Theta) = 0$. Thus, $\bar{C}(\Theta)$ is an arbitrary constant which we are free to choose. From this point onwards, all subsequent results of the recursion are non-unique. This behaviour is mirrored by the recursion (7.11) for the coefficients $C(\Theta)$, at exactly the same singular partitions.

In connection with this non-uniqueness, notice that if $\Theta = \{U_1, U_2, \ldots, U_k\}$ is a singular partition of $U$, then for any choice of the constants $A$, $B$, the variable $Ab(U_1)b(U_2) \cdots b(U_k) + Bb(U)$ satisfies (7.2), and is of the same form as $b(U)$ (see (7.1)).

Singular cases arise when $r(\{U\}) = 1$ for a set of loci $U$, where $|U| > 1$ (a situation referred to as "complete linkage"). Singular cases also arise in certain extreme forms of "interference", where the non-occurrence of recombination among one set of loci implies that there has also been no recombination among some other set of loci.

For a particularly important class of singular cases, see [2]. Baake [2] analysed the dynamics of a population evolving under random union of gametes and recombination. Here, the loci $1, 2, \ldots, n$ are arranged, in ascending order, along a single linear chromosome. Following the union of two haploid gametes, recombination occurs by no more than one "cross-over". Notice that one consequence of this is that if there is no cross-over between loci $i$ and $j$ ($i < j$), then this implies that there must also be no cross-over between loci $i + 1$ and $j - 1$ ($2 < j - i$).

Note that the analysis which follows applies to non-singular cases only. We can economise a little on the proliferation of algebra which arises when we use (7.7) to derive the coefficients $\bar{C}(\Theta)$ recursively, by making use of a reduction formula. For any partition of a set into non-empty disjoint sub-sets, at least one of which contains only a single element (locus)—for example, the partition $\Theta \cup \{\{j\}\}$ of the set $U \cup \{j\}$ (where $\Theta$ is a partition of $U$)—we have the simple reduction formula

$$\bar{C}\left(\Theta \cup \{\{j\}\}\right) = \bar{C}(\Theta)\bar{C}\left(\{\{j\}\}\right). \tag{7.8}$$

For a proof of this reduction formula, see Appendix B. This reduction formula does not apply to singular cases.

Now we turn to the coefficients $C(\Theta)$ in the forward transformation. The recursion for calculating the coefficients $C(\Theta)$, given the $r(\Theta)$, is

$$\left(\left(\prod_{R \in \Theta} r(\{R\})\right) - \lambda(V)\right) C(\Theta)$$

$$= - \sum_{\substack{\Psi : \Theta \prec \Psi \\ \Psi \neq \Theta}} \left(\prod_{A \in \Psi} r(\Theta \overset{\Rightarrow}{\cap} A)\right) C(\Psi), \tag{7.9}$$

where $V = \bigcup_{R \in \Theta} R$. For a derivation of this recursion, see Appendix C.

For the trivial partition of a set into one part (a partition $\Theta$ where $|\Theta| = 1$), (7.9) reduces to

$$\left(\rho(V) - \lambda(V)\right) C(\{V\}) = 0. \tag{7.10}$$

Therefore, if $C(\{V\}) \neq 0$, then $\lambda(V) = r(\{V\})$ for any set of loci $V \neq \emptyset$, as we have already established in (7.6). So, the values of the $C(\{V\}) \neq 0$, must be specified as initial conditions. Substituting (7.6) back into (7.9), we obtain the recursion

$$\left(\left(\prod_{R \in \Theta} r(\{R\})\right) - r(\{V\})\right) C(\Theta)$$

$$= - \sum_{\substack{\Psi : \Theta \prec \Psi \\ \Psi \neq \Theta}} \left(\prod_{A \in \Psi} r(\Theta \overset{\Rightarrow}{\cap} A)\right) C(\Psi). \tag{7.11}$$

From this we can obtain the rest of the $C(\Theta)$.

Now we turn to the relationship between the coefficients $C(\Theta)$ in the forward transformation (7.1) and the coefficients $\bar{C}(\Theta)$ in the inverse transformation (7.3).

By substituting (7.3) into (7.1), and then equating coefficients of the $\prod_{R \in \Theta} b_t(R)$, the following direct relationships between the $C(\Theta)$ and $\bar{C}(\Theta)$ can be derived.

$$1 = \bar{C}(\{V\}) \, C(\{V\}), \tag{7.12a}$$

$$0 = \sum_{\Psi : \Theta \prec \Psi} \left( \prod_{A \in \Psi} \bar{C}(\Theta \overset{\rightarrow}{\cap} A) \right) C(\Psi) \tag{7.12b}$$

(see Appendix D for details). Rearranging (7.12b) yields

$$\left( \bigcup_{R \in \Theta} \bar{C}(\{R\}) \right) C(\Theta) = - \sum_{\substack{\Psi : \Theta \prec \Psi \\ \Psi \neq \Theta}} \left( \prod_{A \in \Psi} \bar{C}(\Theta \overset{\rightarrow}{\cap} A) \right) C(\Psi). \tag{7.13}$$

Provided that $\bar{C}(\{U\}) \neq 0$ for all sets $U \neq \emptyset$, (7.13) determines recursively the values of the coefficient $C(\Theta)$ for all partitions $\Theta$ from the coefficients $\bar{C}(\Theta)$. Therefore, when $\bar{C}(\{U\}) \neq 0$ for all sets $U \neq \emptyset$, the system of recursions (7.13) has a *unique* solution $\{C(\Theta)\}$. This result will play an important role in the forthcoming paper.

The inverse of this relationship between the $C(\Theta)$ and $\bar{C}(\Theta)$ can be obtained directly by substituting (7.1) into (7.3), and then equating coefficients of the $\prod_{R \in \Theta} p_t(R)$. However, because (7.1) and (7.3) are of the same form, it is possible to obtain the inverse relationship immediately from (7.12), by symmetry. Hence the inverse relationship is

$$1 = C(\{V\}) \, \bar{C}(\{V\}), \tag{7.14a}$$

$$0 = \sum_{\Psi : \Theta \prec \Psi} \left( \prod_{A \in \Psi} C(\Theta \overset{\rightarrow}{\cap} A) \right) \bar{C}(\Psi), \tag{7.14b}$$

which rearranges to give the recursion

$$\left( \bigcup_{R \in \Theta} C(\{R\}) \right) \bar{C}(\Theta) = - \sum_{\substack{\Psi : \Theta \prec \Psi \\ \Psi \neq \Theta}} \left( \prod_{A \in \Psi} C(\Theta \overset{\rightarrow}{\cap} A) \right) \bar{C}(\Psi). \tag{7.15}$$

So, by the same argument as before, when $C(\{U\}) \neq 0$ for all sets $U \neq \emptyset$, the system of recursions (7.15) has a *unique* solution $\{\bar{C}(\Theta)\}$.

The variables which Lyubich denotes by $C_{\{U\}}(p(g))$ are identical to Bennett's principle components ($b(U)$ in my notation). It appears that the variables which Lyubich denotes by $C_{\Theta}(p(g))$ must reduce to products of Bennett's variables $\left( \prod_{R \in \Theta} b_t(R) \text{ in my notation} \right)$. However, this is not apparent from Lyubich's own presentation.

## Appendix A

In this appendix, we give a proof of Proposition 1. To prove that the set of conditions (5.2) is equivalent to the set of conditions (5.4), first, notice that (5.2a)–(5.2c) are identical to (5.4a)–(5.4c). Next, (5.2d) we find that

$$R_a \cap U = \bigcup_{b=1}^{d} \left( R_a \cap (R_b \cap A_b) \right) = \bigcup_{b=1}^{d} \left( (R_a \cap R_b) \cap A_b \right)$$

(using the fact that $\cap$ is distributive over $\cup$, then using the fact that $\cap$ is associative). This, together with (5.2c) implies (5.4d). So, the set of conditions (5.2) implies the set of conditions (5.4).

The union of the left-hand sides of (5.4d) over all $a = 1, 2, \ldots, d$ must be identical to the union of the left-hand side of (5.4d) over all $a = 1, 2, \ldots, d$. This immediately gives us

$$\bigcup_{a=1}^{d} (R_a \cap U) = \bigcup_{a=1}^{d} (R_a \cap A_a),$$

and hence

$$\left( \bigcup_{a=1}^{d} R_a \right) \cap U = \bigcup_{a=1}^{d} (R_a \cap A_a)$$

(using the fact that $\cap$ is distributive over $\cup$). This, together with (5.4a) and (5.4b) implies (5.2d). So, we have proved that the set of conditions (5.4) implies the set of conditions (5.2). We now know that (5.2) implies (5.4) and (5.4) implies (5.2). So, the set of conditions (5.2) is equivalent to the set of conditions (5.4).

## Appendix B

In this appendix, we first derive the recursions (7.4) for the $\bar{C}(\Theta)$. Second, we prove the reduction formula (7.8) for the $\bar{C}(\Theta)$.

If we substitute (7.3) into both sides of (6.10), then we obtain

$$\sum_{\Theta \in \pi(V)} \bar{C}(\Theta) \left( \prod_{R \in \Theta} b_{t+1}(R) \right)$$

$$= \sum_{\Psi \in \pi(V)} r(\Psi) \left( \prod_{A \in \Psi} \left( \sum_{\Phi \in \pi(A)} \bar{C}(\Phi) \left( \prod_{R \in \Phi} b_t(R) \right) \right) \right) \tag{B.1}$$

provided that we adopt the convention that $\bar{C}(\{\emptyset\}) = 1$, $b_t(\emptyset) = 1$. If we substitute (7.2) into the left-hand side of (B.1), we have

$$\sum_{\Theta \in \pi(V)} \bar{C}(\Theta) \left( \prod_{R \in \Theta} \lambda(R) \right) \left( \prod_{R \in \Theta} b_t(R) \right)$$

$$= \sum_{\Psi \in \pi(V)} r(\Psi) \left( \prod_{A \in \Psi} \left( \sum_{\Phi \in \pi(A)} \bar{C}(\Phi) \left( \prod_{R \in \Phi} b_t(R) \right) \right) \right). \tag{B.2}$$

Expanding out the product on the right-hand side, we obtain

$$\prod_{A \in \Psi} \left( \sum_{\Phi \in \pi(A)} \bar{C}(\Phi) \left( \prod_{R \in \Phi} b_t(R) \right) \right)$$

$$= \sum_{\Theta : \Theta \prec \Psi} \left( \prod_{A \in \Psi} \bar{C}(\Theta \overset{\Rightarrow}{\cap} A) \right) \left( \prod_{R \in \Theta} b_t(R) \right). \tag{B.3}$$

(Hint: compare this with (3.1).) Now, if we substitute this back into the right-hand side of (B.2), we obtain

$$\sum_{\Theta \in \pi(V)} \bar{C}(\Theta) \left( \prod_{R \in \Theta} \lambda(R) \right) \left( \prod_{R \in \Theta} b_t(R) \right)$$

$$= \sum_{\Psi \in \pi(V)} r(\Psi) \left( \sum_{\substack{\Theta : \Theta \in \pi(V) \\ \Theta \prec \Psi}} \left( \prod_{A \in \Psi} \bar{C}(\Theta \overset{\Rightarrow}{\cap} A) \right) \left( \prod_{R \in \Theta} b_t(R) \right) \right)$$

$$= \sum_{\Theta \in \pi(V)} \left( \sum_{\substack{\Psi : \Psi \in \pi(V) \\ \Psi : \Theta \prec \Psi}} r(\Psi) \left( \prod_{A \in \Psi} \bar{C}(\Theta \overset{\Rightarrow}{\cap} A) \right) \right) \left( \prod_{R \in \Theta} b_t(R) \right). \tag{B.4}$$

So, equating coefficients of the $\prod_{R \in \Theta} b_t(R)$ in (B.4) gives

$$\left( \prod_{R \in \Theta} \lambda(R) \right) \bar{C}(\Theta) = \sum_{\Psi : \Theta \prec \Psi} r(\Psi) \left( \prod_{A \in \Psi} \bar{C}(\Theta \overset{\Rightarrow}{\cap} A) \right). \tag{B.5}$$

By a small rearrangement, we obtain the recursion (7.4) as required.

The proof of this reduction formula (7.8) (which does not apply to singular cases) is as follows. For a partition of the form $\Theta \cup \{\{j\}\}$, (7.4) can be written in the form

$$r(\{j\}) \left( \prod_{R \in \Theta} r(\{R\}) \right) \bar{C}(\Theta \cup \{\{j\}\})$$

$$= \sum_{\Psi : \Theta \prec \Psi} r(\Psi \cup \{\{j\}\}) \left( \prod_{A \in \Psi} \bar{C}((\Theta \cup \{\{j\}\}) \overset{\Rightarrow}{\cap} A) \right) \bar{C}((\Theta \cup \{\{j\}\}) \overset{\Rightarrow}{\cap} \{j\})$$

$$+ \sum_{\Psi:\Theta \prec \Psi} \left( \sum_{B:B \in \Psi} r\left(\Psi \cup (B \cup \{j\}) - \{B\}\right) \right.$$

$$\left. \times \left( \prod_{B \in \Psi - \{B\}} \bar{C}\big((\Theta \cup \{\{j\}\}) \stackrel{\Rightarrow}{\cap} A\big) \right) \right) \bar{C}\big((\Theta \cup \{\{j\}\}) \stackrel{\Rightarrow}{\cap} (B \cup \{j\})\big)$$

$$= \sum_{\Psi:\Theta \prec \Psi} r\left(\Psi \cup \{\{j\}\}\right) \left( \prod_{A \in \Psi} \bar{C}(\Theta \stackrel{\Rightarrow}{\cap} A) \right) \bar{C}\left(\{\{j\}\}\right)$$

$$+ \sum_{\Psi:\Theta \prec \Psi} \left( \sum_{B:B \in \Psi} r\left(\Psi \cup (B \cup \{j\}) - \{B\}\right) \right.$$

$$\left. \times \left( \prod_{A \in \Psi - \{B\}} \bar{C}(\Theta \stackrel{\Rightarrow}{\cap} A) \right) \right) \bar{C}\left(\{B, \{j\}\}\right). \tag{B.6}$$

Recall (from 7.6) that $r\left(\{\{j\}\}\right) = 1$. If the reduction formula (7.8) is true, then (B.6) is equivalent to (implies and is implied by)

$$\left( \prod_{R \in \Theta} r\left(\{R\}\right) \right) \bar{C}(\Theta) \bar{C}\left(\{\{j\}\}\right)$$

$$= \bar{C}\left(\{\{j\}\}\right) \sum_{\Psi:\Theta \prec \Psi} \left( r\big(\Psi \cup \{\{j\}\}\big) + \sum_{B:B \in \Psi} r\big(\Psi \cup (B \cup \{j\}) - \{B\}\big) \right)$$

$$\times \left( \prod_{A \in \Psi} \bar{C}(\Theta \stackrel{\Rightarrow}{\cap} A) \right), \tag{B.7}$$

from which $\bar{C}\left(\{\{j\}\}\right)$ cancels out, leaving

$$\left( \prod_{R \in \Theta} r\left(\{R\}\right) \right) \bar{C}(\Theta)$$

$$= \sum_{\Psi:\Theta \prec \Psi} \left( r\big(\Psi \cup \{\{j\}\}\big) + \sum_{B:B \in \Psi} r\big(\Psi \cup (B \cup \{j\}) - \{B\}\big) \right)$$

$$\times \left( \prod_{A \in \Psi} \bar{C}(\Theta \stackrel{\Rightarrow}{\cap} A) \right). \tag{B.8}$$

By (2.3)

$$r\big(\Psi \cup \{\{j\}\}\big) + \sum_{B:B \in \Psi} r\big(\Psi \cup (B \cup \{j\}) - \{B\}\big) = r\left(\Psi\right). \tag{B.9}$$

So (B.8) reduces to (7.4) for $\bar{C}(\Theta)$. Therefore, the reduction formula (7.8) together with the recursion (7.4) for $\bar{C}(\Theta)$ implies the recursion (7.4) for $\bar{C}(\Theta \cup \{\{j\}\})$.

So, if for any partition $\Theta$, we have a set of $\bar{C}(\Phi)$, $\Phi \subset \Theta$, that satisfy the system (7.4), then formula (7.8) enables us to construct a set of $\bar{C}(\Phi)$, $\Phi \subset \Theta \cup \{\{j\}\}$, which also satisfies the system (7.4).

However, given "boundary conditions" specifying the values of the $\bar{C}(\Phi)$ for all $\Phi$ having $|\Phi| = 1$, the system (7.4) has a *unique* solution, except in singular cases. (This is obvious from its recursive form.) Therefore, the solution $\{\bar{C}(\Phi)\}$ of the system (7.4) for $\Phi \subset \Theta \cup \{\{j\}\}$, constructed (from the solution for $\Phi \subset \Theta$) using formula (7.8), must be the *unique* solution of the system (7.4) for $\Phi \subset \Theta \cup \{\{j\}\}$. This argument holds true for any partition $\Theta$. Therefore, for every partition $\Theta$, the solution $\{\bar{C}(\Phi)\}$, $\Phi \subset \Theta$ of the system (7.4) must satisfy the reduction formula (7.8). This completes the proof of the reduction formula (7.8) for non-singular cases.

## Appendix C

In this appendix, we derive the recursions (7.9) for the $C(\Theta)$. Substitute (7.1) into both sides of (7.2) to obtain

$$\sum_{\Psi \in \pi(V)} C(\Psi) \left( \prod_{A \in \Psi} p_{t+1}(A) \right) = \lambda(V) \sum_{\Theta \in \pi(V)} C(\Theta) \left( \prod_{R \in \Theta} p_t(R) \right). \qquad \text{(C.1)}$$

Substitute (6.10) into the left-hand side of (C.1) to obtain

$$\sum_{\Psi \in \pi(V)} C(\Psi) \left( \prod_{A \in \Psi} \left( \sum_{\Phi \in \pi(A)} r(\Phi) \left( \prod_{R \in \Phi} p_t(R) \right) \right) \right)$$
$$= \lambda(V) \sum_{\Theta \in \pi(V)} C(\Theta) \left( \prod_{R \in \Theta} p_t(R) \right). \qquad \text{(C.2)}$$

Expanding out the product on the left-hand side of (C.2), we obtain

$$\prod_{A \in \Psi} \left( \sum_{\Phi \in \pi(A)} r(\Phi) \left( \prod_{R \in \Phi} p_t(R) \right) \right)$$
$$= \sum_{\Theta : \Theta \prec \Psi} \left( \prod_{A \in \Psi} r(\Theta \stackrel{\rightarrow}{\cap} A) \right) \left( \prod_{R \in \Theta} p_t(R) \right). \qquad \text{(C.3)}$$

The above expansion is exactly similar to that in (B.3). Now, if we substitute this back into the left-hand side of (C.2), we obtain

$$\sum_{\Psi \in \pi(V)} C(\Psi) \left( \sum_{\substack{\Theta : \Theta \in \pi(V) \\ \Theta \prec \Psi}} \left( \prod_{A \in \Psi} r(\Theta \overrightarrow{\cap} A) \right) \left( \prod_{R \in \Theta} p_t(R) \right) \right)$$

$$= \sum_{\Theta \in \pi(V)} \left( \sum_{\substack{\Psi : \Psi \in \pi(V) \\ \Theta \prec \Psi}} \left( \prod_{A \in \Psi} r(\Theta \overrightarrow{\cap} A) \right) C(\Psi) \right) \left( \prod_{R \in \Theta} p_t(R) \right)$$

$$= \lambda(V) \sum_{\Theta \in \pi(V)} C(\Theta) \left( \prod_{R \in \Theta} p_t(R) \right). \tag{C.4}$$

Equating coefficients of the $\prod_{R \in \Theta} p_t(R)$, we obtain

$$\lambda \left( \bigcup_{R \in \Theta} R \right) C(\Theta) = \sum_{\Psi : \Theta \prec \Psi} \left( \prod_{A \in \Psi} r(\Theta \overrightarrow{\cap} A) \right) C(\Psi). \tag{C.5}$$

This can be rearranged to give the recursion (7.9) for the $C(\Theta)$.


## Appendix D

In this appendix, we derive the direct relationship (7.12) between the $C(\Theta)$ and $\bar{C}(\Theta)$. Substituting (7.3) into the right-hand side of (7.1), we obtain

$$b_t(V) = \sum_{\Psi \in \pi(V)} C(\Psi) \left( \prod_{A \in \Psi} \left( \sum_{\Phi \in \pi(A)} \bar{C}(\Phi) \left( \prod_{R \in \Phi} b_t(R) \right) \right) \right). \tag{D.1}$$

Now, expand out the product on the right-hand side of (D.1) (exactly as in (B.3)). Then substituting this back into the right-hand side of (D.1), we obtain

$$b_t(V) = \sum_{\Psi \in \pi(V)} C(\Psi) \left( \sum_{\Theta : \Theta \prec \Psi} \left( \prod_{A \in \Psi} \bar{C}(\Theta \overrightarrow{\cap} A) \right) \left( \prod_{R \in \Theta} b_t(R) \right) \right)$$

$$= \sum_{\Theta \in \pi(V)} \left( \sum_{\Psi : \Theta \prec \Psi} C(\Psi) \left( \prod_{A \in \Psi} \bar{C}(\Theta \overrightarrow{\cap} A) \right) \right) \left( \prod_{R \in \Theta} b_t(R) \right). \tag{D.2}$$

Now we equate coefficients of the $\prod_{R \in \Theta} b_t(R)$ in (D.2). Equating the coefficients of $b_t(V)$, we obtain (7.12 a). Equating the coefficients of $\prod_{R \in \Theta} b_t(R) \neq b_t(V)$, we obtain (7.12 b).

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