Supplementary Online Material for "Evolution in structured populations: beyond the kin/group debate"

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January 12, 2011

This appendix provides an expanded treatment of the material discussed in Box 1-5 in the main text.

S1 General mathematical background

Consider an asexual organism with a trait, z, that is determined by a single, diallelic locus ('A' and 'a'). Suppose that 'a' individuals have phenotype $\hat{z}$ and 'A' individuals have phenotype $\hat{z}+\delta$ (i.e., δ is the effect, on the phenotype, of carrying allele 'A'). Generally, we can write the phenotype of an individual as $z=\hat{z}+\delta x$, where x is an indicator variable for an individual's genotype (it equals 1 if the individual carries allele 'A' and zero otherwise). For simplicity we assume that the population is very large, and that individuals can be characterized by their genotype only, i.e there is no age or stage structure. The rate of change of the frequency of allele A (which is simply $\bar{x}$, the average genotype value) is (Crow and Kimura, 1970; Rousset and Billiard, 2000; Rousset, 2004; Taylor et al., 2007*b*; Day and Gandon, 2007)

$$\frac{d\bar{x}}{dt}=\bar{x}(1-\bar{x})S-uM \tag{S1}$$

where S is the selection coefficient, u is the mutation rate, and M is a mutation term that depends in general on the correlation between mutation and reproduction. There are two useful ways we can express the selection coefficient. The first is the slope of the regression of an individual's fitness, w, on its genotype, across all individuals in the population; i.e., $S=\mathrm{cov}(w,x)/\mathrm{var}(x)$. The second is the difference in expected fitness between the two alleles (Crow and Kimura, 1970; Frank, 1998; Rousset, 2004). With the regression formulation, equation (S1) is a version of Price's equation with mutation (Taylor et al., 2007*b*; Day and Gandon, 2007), and it is essentially the same description recently used in Nowak et al. (2010), using a slightly different mathematical approach.

Now let us assume that the mutation rate is low ($u=0$). Suppose that z represents the amount of help provided to others, and that each individual interacts with n other individuals, and for simplicity we assume that no help can be provided to oneself. Thus the fitness of the i^{th} individual depends on its own phenotype, indicated by $z_\bullet$ and on the phenotype of n other individuals, and is given by $w_i(z_i;z_{i1},\dots,z_{in})$. The first argument indicates the level of help provided by the focal individual, and z_{ij} indicates the level of help received from the j^{th} individual with which it interacts. To make this precise we need to specify an explicit population structure such that, for any individual in the population, we can unambiguously identify its 1^{st}, 2^{nd}, ... up to n^{th} interactor. For example, we might specify a deme structure with demes of size $n+1$ (Rousset and Billiard, 2000), we might specify pair-wise interactions, or interactions might be specified by a graph (Taylor et al., 2007*a*). For the present purposes we need not be explicit about this structure, and in fact in much of the literature the structure is often not made explicit (see Box 4 in the main text).

The selection coefficient is difficult to evaluate explicitly in general, but suppose that fitness is linear in phenotype as well as in the genotype of the interactor (i.e. $w_i=-C(\hat{z}+\delta x_i)+B_1(\hat{z}+\delta x_{i1})+\cdots+B_n(\hat{z}+\delta x_{in})$, where C is the unit cost of providing help, and B_i is the unit benefit obtained by individual i providing help). Here, we have assumed that the genetic structure is rigid and regular, in the sense that all individuals have the same number and types of interactions, so that the constants B_j

are the same for each focal individual, but this assumption can be relaxed (Taylor, 2009). Calculating the difference in expected fitness between the two alleles we obtain

$$S = [-C + B_1R_1 + \cdots + B_nR_n]\delta \tag{S2}$$

where $R_j = \rho^j_{A/A} - \rho^j_{A/a}$, and $\rho^j_{A/A}$ (resp. $\rho^j_{A/a}$) denotes the probability that the neighbour involved in the j^{th} interaction of an 'A' (resp. 'a) individual carries the 'A' allele. Note that, because the selection coefficient can also be written as $S = \mathrm{cov}(w(\hat{z}+\delta x; z_1, \dots, z_n), x)/\mathrm{var}(x)$, we can obtain an alternative formula for R_j as $R_j = \mathrm{cov}(x, x_j)/\mathrm{var}(x)$. Still another way to express R_j is $R_j = (\rho^j_{A/A} - \bar{x})/(1-\bar{x})$ because $\bar{x} = \bar{x}\rho^j_{A/A} + (1-\bar{x})\rho^j_{A/a}$ (Day and Taylor, 1998).

Although we need to know the probability distribution of different genotypic interactions to calculate s in the general case, expression (S2) shows that we need only know the first moments of this distribution when fitness is a linear function of genotype. If we further assume that selection is weak, then the R's can be calculated under the assumption that allele 'A' is neutral and the Rs can be determined, or measured, independent of the mutation process (Rousset and Billiard, 2000; Taylor et al., 2007*b*). They can then be interpreted as the genealogical relatedness between individuals (Taylor, 1989, 1996; Rousset, 2002, 2004). The term $-C$ is referred to as the direct fitness effect of the allele, and expresses the cost to an individual of providing help. The remaining terms are referred to as the indirect fitness effects, and express the benefit of receiving help from others.

A special case of interest is where all n individuals have the same relationship to the focal individual (e.g., group structured populations), giving

$$S = (-C + nBR)\delta. \tag{S3}$$

For such situations, the MS methodology can then also be applied since we can view the $n+1$ interacting individuals as forming a group. Using the regression formulation of the selection coefficient, we can then decompose the covariance term to give (Queller, 1992; Frank, 1998)

$$S = \frac{\mathrm{E}[\mathrm{cov}_g(w,x)]}{\mathrm{var(x)}} + \frac{\mathrm{cov}(\bar{w}_g, \bar{x}_g)}{\mathrm{var(x)}} \tag{S4}$$

where the first term is the covariance of individual fitness, w, with genotype, within each group, g, averaged over all groups, and the second term is the covariance of mean group fitness, $\bar{w}_g$, with mean group allele frequency, $\bar{x}_g$, across all groups. Thus the first term represents within-group selection, while the second represents between-group selection.

The relationship between the IF and MS methodologies can now be better understood by substituting the above linear expression for fitness into (S4). The selection coefficient can then be written as a sum of four components, corresponding to the different combinations of direct/indirect and within/between-group effects. Each methodology simply differs in how these four components are grouped, according to the following table:

$$\begin{array}{lcccc}
 & \textbf{Direct} & \textbf{Indirect} & & \\
\textbf{Within-group} & -C\dfrac{\mathrm{E}[\mathrm{var}_g(x)]}{\mathrm{var(x)}} & nB\dfrac{\mathrm{E}[\mathrm{cov}_g(x,y)]}{\mathrm{var(x)}} & \Rightarrow & \dfrac{\mathrm{E}[\mathrm{cov}_g(w,x)]}{\mathrm{var}(x)} \\
\textbf{Between-group} & -C\dfrac{\mathrm{var}(\bar{x}_g)}{\mathrm{var}(x)} & nB\dfrac{\mathrm{cov}(\bar{x}_g,\bar{y}_g)}{\mathrm{var}(x)} & \Rightarrow & \dfrac{\mathrm{cov}(\bar{w}_g,\bar{x}_g)}{\mathrm{var}(x)} \\
 & \Downarrow & \Downarrow & & \\
 & -C & nBR & &
\end{array}$$

where y is the genotype of a randomly selected group member for the focal individual.

The assumptions used above are interrelated in that one can often impose a weak selection assumption is such a way that it automatically makes fitness approximately linear in the phenotype (Taylor and Frank, 1996; Taylor et al., 2007*b*). For example, in the above model, if we assume δ is small, then selection will be weak. At the same time, fitness will also be approximately linear because we can then expand w in a Taylor series to get $B_j = \partial w/\partial z_{ij}$ and $-C = \partial w/\partial z_i$. This need not be true for all forms of weak selection (Wild and Traulsen, 2007), however, and therefore the assumptions on linearity and weak selection should be viewed as distinct.

Lastly, it is worth stressing that the above expressions for the selection coefficient clearly need not correctly predict the direction of selection if any of the assumptions employed fail to hold. Indeed, there has been considerable interest in exploring how predictions are altered when other assumptions are made, including finite population sizes (Rousset and Billiard, 2000; Taylor et al., 2007*b*), fluctuating demography (appendix S2; Rousset and Ronce (2004); Lehmann et al. (2006); Lion and Gandon (2009)), non-linear genotype-phenotype maps (e.g. dominance, Roze and Rousset (2003)), or non-pairwise interactions (Ohtsuki, 2010). Theoretical results in IF theory demonstrate that these effects can be accounted for through additional terms (Queller, 1992; Rousset and Ronce, 2004; Lehmann et al., 2006), or by considering triplets instead of pairs of genes. (Roze and Rousset, 2003; Lessard, 2007; Lessard and Lahaie, 2009; Ohtsuki, 2010).

S2 Demographic and genetic structuring

Consider an extension of the previous model, in which individuals live on a network of sites. Suppose that each site of the network can be either empty or occupied by one individual, and that it is connected to n other such sites. We use $q_{o/k}$ to denote the average fraction of the n local sites that are empty, as experienced by a site in state k, and $q_{A/k}$ (resp. $q_{a/k}$) to denote the average fraction of local sites harbouring an 'A' (resp. 'a') individual, as experienced by a site in state k. As in Section 1 in the main text, an individual with genotype x has its death rate increased by an amount $C(\hat{z}+\delta x)$ as a result of the help it provides, but decreased by an amount $B(\hat{z}+\delta x_i)$ for each neighbour that provides it help. The death rates are therefore

$$\begin{aligned} d_A &= d + C(\hat{z}+\delta) - B(\hat{z}+\delta)nq_{A/A} - B\hat{z}nq_{a/A} + 0\ nq_{o/A} \\ d_a &= d + C\hat{z} \qquad\quad - B(\hat{z}+\delta)nq_{A/a} - B\hat{z}nq_{a/a} + 0\ nq_{o/a} \end{aligned}$$

where $q_{A/k}+q_{a/k}+q_{o/k}=1$. We have included '0' terms to highlight the fact that, if there are empty sites next to an individual, this effectively results in a loss of help, over and above the difference in help provided by 'A' versus 'a' individuals. Suppose that each individual produces offspring at a rate proportional to the number of empty neighbouring sites. As we discuss in the main text, this is only one possible form of density-dependence, but it is sufficient to illustrate some important points. Thus the birth rates are $bq_{o/A}$ and $bq_{o/a}$. The selection coefficient is then

$$S = b(q_{o/A}-q_{o/a}) + [-C + Bn(q_{A/A}-q_{A/a})]\delta - B\hat{z}n(q_{o/A}-q_{o/a}).$$

The differences in local densities $q_{A/A}-q_{A/a}$ and $q_{o/A}-q_{o/a}$ depend on the action of the 'A' allele, and therefore even with additive fitness effects, demographic and genetic structuring interact in potentially complex ways.

The quantity $q_{A/A}-q_{A/a}$ measures the extent to which 'A' alleles are more abundant in the neighbourhood of other 'A' alleles than of 'a' alleles, and has a long history. In the early group selection literature, it was termed "difference in subjective frequencies" (Wilson, 1977), and it has been recently characterised as an assortment measure (Fletcher and Doebeli, 2009). When selection is weak we can calculate this measure under neutrality, and thereby give it a precise genetic interpretation (Lion and Gandon, 2009; Lion, 2009). Under neutrality,

$$q_{A/A}-q_{A/a} = q_{\times/\times}\frac{\rho_{A/A}-\bar{x}}{1-\bar{x}} = q_{\times/\times}R.$$

The right-hand side separates two effects: a demographic effect ($q_{\times/\times}$ is the local density of occupied sites experienced by an individual of any genotype and is therefore a measure of habitat saturation) and a genetic effect. Indeed, $\rho_{A/A}$ is the frequency of 'A' neighbours among the occupied sites in the neighbourhood of an 'A' allele, so that $R=(\rho_{A/A}-\bar{x})/(1-\bar{x})$ measures genealogical relatedness (Boxes 1 and 3 in the main text). Hence, under weak selection, the selection gradient reduces to

$$S = [(-C + nq_{\times/\times}BR) + (b - nB\hat{z})\Delta q_o]\delta \tag{S5}$$

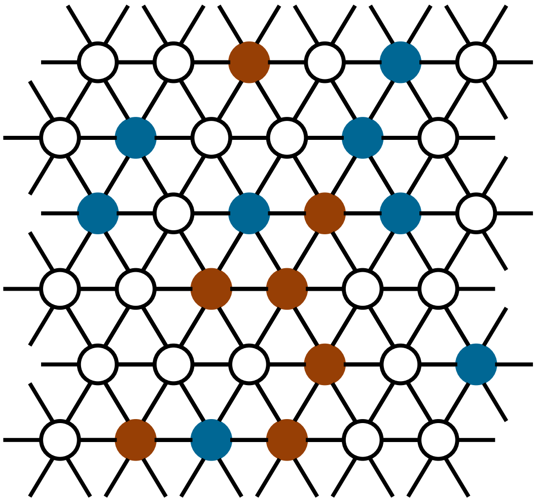

Figure 1: Demographic and genetic structuring on a network. Sites can be either empty (open circles) or occupied by an individual carrying allele ‘A‘ (red circles) or ‘a‘ (blue circles). In this example, each site is connected to $n = 6$ other sites.

where Δq_o is the first-order effect of selection on $q_{o/A} - q_{o/a}$. Thus, under additivity and weak selection, the selection coefficient separates into conceptually distinct components representing genetic structuring (i.e., R), demographic structuring ($q_{\times/\times}$), and a demographic effect that will generally depend on the interplay between genetic and demographic structuring ($q_{o/A} - q_{o/a}$). Note that a biological interpretation can again be had as a form of Hamilton's rule (van Baalen and Rand, 1998; Lion and Gandon, 2009), in which the relatedness R can be given a genealogical interpretation.

As discussed in the main text, the first term of equation (S5) has a similar form to equation (S3), but the second term of equation (S5) represents two additional selective effects due to the effect of mutation on demographic structuring. The first selective effect, $b\Delta q_o$, measures the difference in the availability of empty sites between 'A' and 'a' alleles (or, in other words, the differential competition between the two alleles for empty space). This comes from the density-dependence of reproduction, which is now explicit because the present model is necessarily a 'closed' model (Box 4 in the main text). The second selective effect, $-B\hat{z}\Delta q_o$, accounts for the fact that having empty sites in one's neighbourhood represents a net loss in helping opportunities, and measures the differences between the two alleles in this demographic effect. Unfortunately, even in this case, the computation of Δq_o requires additional assumptions (e.g., a first-order approximation in space; Lion and Gandon (2009, 2010)). In general, this additional term due to demographic fluctuations will also depend on measures of genetic structuring such as relatedness (Rousset and Ronce, 2004; Lion and Gandon, 2009, 2010; Lehmann and Rousset, 2010).

References

Crow, J. F. and Kimura, M., 1970. An Introduction to Population Genetics Theory. Burgess Publishing Company, Minneapolis, MN, USA.

Day, T. and Gandon, S. 2007. Applying population-genetic models in theoretical evolutionary epidemiology. Ecol. Lett. 10:876–888.

Day, T. and Taylor, P. D. 1998. Unifying genetic and game theoretic models of kin selection for continuous traits. J. theor. Biol. 194:391–407.

Fletcher, J. A. and Doebeli, M. 2009. A simple and general explanation for the evolution of altruism. Proc. Roy. Soc. Lond. B 276:13–19.

Frank, S. A., 1998. Foundations of social evolution. Princeton University Press, Princeton, NJ, USA.

Lehmann, L., Perrin, N., and Rousset, F. 2006. Population demography and the evolution of helping behaviours. Evolution 60:1137–1151.

Lehmann, L. and Rousset, F. 2010. How life history and demography promote or inhibit the evolution of helping behaviours. Phil. Trans. Roy. Soc. B 365:2599–2617.

Lessard, S. 2007. Cooperation is less likely to evolve in a finite population with a highly skewed distribution of family size. Proc. Roy. Soc. Lond. B 274:1861–1865.

Lessard, S. and Lahaie, P. 2009. Fixation probability with multiple alleles and projected average allelic effect on selection. Theor. Pop. Biol. 75:266–277.

Lion, S. 2009. Relatedness in spatially structured populations with empty sites: an approach based on spatial moment equations. J. theor. Biol. 260:121–131.

Lion, S. and Gandon, S. 2009. Habitat saturation and the spatial evolutionary ecology of altruism. J. evol. Biol. 22:1487–1502.

Lion, S. and Gandon, S. 2010. Life history, habitat saturation and the evolution of fecundity and survival altruism. Evolution 64:1594–1606.

Nowak, M. A., Tarnita, C. E., and Wilson, E. O. 2010. The evolution of eusociality. Nature 466:1057–1062.

Ohtsuki, H. 2010. Evolutionary games in wright's island model: kin selection meets evolutionary game theory. Evolution .

Queller, D. C. 1992. Quantitative genetics, inclusive fitness, and group selection. Am. Nat. 139:540–558.

Rousset, F. 2002. Inbreeding and relatedness coefficients: what do they measure? Heredity 88:371–380.

Rousset, F., 2004. Genetic structure and selection in subdivided populations. Princeton University Press, Princeton, NJ, USA.

Rousset, F. and Billiard, S. 2000. A theoretical basis for measures of kin selection in subdivided populations: finite populations and localized dispersal. J. evol. Biol. 13:814–825.

Rousset, F. and Ronce, O. 2004. Inclusive fitness for traits affecting metapopulation demography. Theor. Pop. Biol. 65:127–41.

Roze, D. and Rousset, F. 2003. Selection and drift in subdivided populations : a straightforward method to derive diffusion approximations, a applications involving dominance, selfing and local extinctions. Genetics 165:2153–2166.

Taylor, P. D. 1989. Evolutionary stability in one-parameter models under weak selection. Theor. Pop. Biol. 36:125–143.

Taylor, P. D. 1996. Inclusive fitness arguments in genetic models of behaviour. J. math. Biol. 34:654–674.

Taylor, P. D. 2009. Decompositions of Price's formula in an inhomogeneous population. J. evol. Biol. 22:201–213.

Taylor, P. D., Day, T., and Wild, G. 2007*a*. Evolution of cooperation in a finite homogeneous graph. Nature 447:469–472.

Taylor, P. D., Day, T., and Wild, G. 2007*b*. From inclusive fitness to fixation probability in homogeneous structured populations. J. theor. Biol. 249:101–110.

Taylor, P. D. and Frank, S. A. 1996. How to make a kin selection model? J. theor. Biol. 180:27–37.

van Baalen, M. and Rand, D. A. 1998. The unit of selection in viscous populations and the evolution of altruism. J. theor. Biol. 193:631–648.

Wild, G. and Traulsen, A. 2007. The different limits of weak selection and the evolutionary dynamics of finite populations. J. theor. Biol. 247:382–390.

Wilson, D. S. 1977. Structured demes and the evolution of group-advantageous traits. Am. Nat. 111:157–186.