

# Local founding events as determinants of genetic structure in a plant metapopulation

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The genetic structure of a metapopulation of the weedy plant, *Silene alba*, was quantified by calculating  $F_{ST}$ , Wright's measure of the among-deme component of genetic variance, for seven polymorphic allozyme loci and a chloroplast DNA (cpDNA) polymorphism. Specifically,  $F_{ST}$  was estimated separately for 12 recently founded demes and 11 demes that had been established in the same area for at least six years, in order to assess the influence of founding events on genetic structure. The  $F_{ST}$  value for the recently established populations was the larger of the two estimates for six of the seven allozyme polymorphisms and for the cpDNA polymorphism, showing that the metapopulation dynamics of extinction and colonization enhance genetic structure. Combined with an estimate of  $k$ , the size of colonizing groups, the  $F_{ST}$  values were also used to estimate  $\phi$ , the probability that two alleles found in a colonizing group originated in the same source population. Information from allozymes and cpDNA resulted in estimates of  $\phi$  of 0.73 and 0.89, respectively, suggesting that relatively little mixing of individuals from diverse source populations occurs during colonization.

**Keywords:** colonization, gene flow, metapopulation, population structure, *Silene alba*.

## Introduction

A metapopulation can be defined as a set of populations in which the individual demes are subject to frequent loss, owing to local extinction, and frequent replacement, owing to colonization (Levins, 1970; Hanski & Gilpin, 1991). When colonization rates are sufficient to offset extinction, the metapopulation can be expected to persist for much longer than any one of its constituent local demes. Recently, there has been considerable interest in the genetic properties of metapopulations, particularly in the influence of frequent extinction and colonization events on the maintenance of genetic variation, and the way that variation is distributed within and among local demes (Slatkin, 1977; Maruyama & Kimura, 1980; Wade & McCauley, 1988; Whitlock & McCauley, 1990; Gilpin, 1991; McCauley, 1991, 1993).

In a metapopulation with high turnover, most demes would be expected to be a relatively few generations removed from their respective founding events. In that case the genetic properties of the metapopulation as a whole would be determined primarily by demographic processes associated with

colonization, and only secondarily by evolutionary pressures acting on local demes after they become established. Several models have illustrated, however, that the genetic consequences of founding events can be complex and depend both on the number of individuals involved in the typical founding event and on the number of source populations from which they are drawn (Slatkin, 1977; Wade & McCauley, 1988; Whitlock & McCauley, 1990). Slatkin (1977) defined two modes of colony formation that represent the extremes of a continuum of possible ways that colonies might form. In the 'migrant pool' mode genes are drawn individually and at random from all possible source populations in order to comprise a given founding event. Colonization then involves an element of gene flow in the sense that genes from various localities are mixed during the colonization process. In contrast, during the 'propagule pool' mode of colonization all of the individuals (and thus all gene copies) that comprise a given founding group are drawn from just one of the possible source populations. Colonization does not involve the mixing of genotypes from different localities. Whitlock & McCauley (1990) generalized this concept by defining a term,  $\phi$ , as the probability that two alleles in a newly formed population were drawn from the same source. Thus,  $\phi = 0$  is equiva-

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lent to the migrant pool and  $\phi = 1$  is equivalent to the propagule pool mode of colonization.

The influence of the mode of colonization on genetic structure is evident by considering the genetic variation expected among a group of newly founded populations. Whitlock & McCauley (1990, eqn 4) show that

$$f_0 = 1/2k + \phi(1 - 1/2k)(1/2N + (1 - 1/2N)f_c), \quad (1)$$

where  $k$  is the number of individuals that comprise a colonizing group,  $N$  is the size of established local populations,  $f_0$  is the probability of identity of alleles within a founding group, and  $f_c$  is the probability that two alleles drawn from the same source population are identical by descent. In this equation  $f_0$  can be considered to represent the genetic structure of a group of recently founded populations and  $f_c$  the genetic structure of the rest of the metapopulation. If the gene copies involved in colonization are drawn at random from within source populations then  $f_0$  is equivalent to Wright's (1978)  $F_{ST}$  as defined only among new populations ( $F_{ST0}$ ) and  $f_c$  is equivalent to Wright's  $F_{ST}$  defined among established populations ( $F_{STc}$ ) (Whitlock & McCauley, 1990). Assuming that  $N \gg k$ , eqn 1 can then be approximated by

$$F_{ST0} = 1/2k + \phi(1 - 1/2k)(F_{STc}). \quad (2)$$

Thus, it can be seen that as  $\phi$  tends to zero the genetic structure of a set of recently established populations is determined primarily by the number of individuals involved in colonization events. The mixing of genotypes from the different sources of colonists destroys any genetic structure extant in the metapopulation and limits overall population differentiation. As  $\phi$  tends to one there is little mixing and colonization amplifies the genetic structure already present in the metapopulation.

In nature, colonization and its impact on genetic structure can be difficult to study directly (McCauley, 1989; Whitlock, 1992). However, eqn 2 might be used to draw inferences about the mode of colonization in natural populations whose demography approximates the assumptions of the model. For example, if estimates of  $k$ ,  $F_{STc}$ , and  $F_{ST0}$  were available for a natural metapopulation, one could solve for  $\phi$  and estimate the amount of mixing that accompanies the colonization process. Further, estimates of  $F_{ST}$  are typically based on information from several genetic markers. If  $F_{STc}$  were to display real variation among genetic markers, eqn 2 also predicts that there should be a correlation between marker-specific values of  $F_{ST0}$  and  $F_{STc}$  as  $\phi$  tends to 1. Thus, any correspondence between marker-specific values of  $F_{ST0}$  and  $F_{STc}$  estimated from

natural populations would be an additional indication that only limited mixing of genes from different localities occurs during colonization.

*Silene alba* (Caryophyllaceae), a dioecious short-lived perennial, is a species of plant whose demography resembles that considered by metapopulation models. This weedy species grows in patches along roadsides and in pastures; patches that are known to undergo a high rate of extinction and colonization (Antonovics *et al.*, 1994; Thrall & Antonovics, 1995). Repeated roadside censuses (Antonovics *et al.*, 1994) have allowed the identification of the size of recently founded populations. Further, McCauley (1994) has used both allozyme and chloroplast DNA (cpDNA) genetic markers to estimate the genetic structure of *S. alba* and has shown a moderate degree of structuring of the allozyme polymorphism and a much larger degree of structuring of the cpDNA polymorphism among established populations. Thus, estimates of  $k$  and  $F_{STc}$  are available.

In this paper the influence of local founding events on genetic structure is evaluated by estimating  $F_{ST0}$  from both allozyme and cpDNA allele frequency variation among 12 local demes of *S. alba* known to have been founded between 1991 and 1994. These  $F_{ST0}$  values are then combined with estimates of  $k$  and  $F_{STc}$  in order to estimate  $\phi$ , the amount of mixing that accompanies colonization. The magnitudes of  $F_{ST0}$  and  $F_{STc}$  are also compared in order to establish whether the net effect of extinction and recolonization in this system is to increase or decrease the among-deme component of genetic variation, relative to a case with no population turnover.

## Materials and methods

Local populations of *S. alba* have been censused since 1988 in the vicinity of the Mountain Lake Biological Station in Giles County, Virginia. Antonovics *et al.* (1994) describe the methods and discuss the results of the first several years of this study, which has been continued since that report. Briefly, populations are censused by driving and walking along approximately 150 km of roadside in early June. At this time the plants are in peak flower and most easily recognized. The census route is divided into arbitrary 40 m intervals on either side of the road. For each interval, for each year, records are available as to the presence or absence of *S. alba*. If *S. alba* is present the numbers of each sex are recorded. From these records both the extinction of this plant at the level of intervals, as well as the colonization of unoccupied intervals, are seen fairly fre-

quently (Antonovics *et al.*, 1994). Thus, within the metapopulation there are demes, defined at the level of the interval, which range in age from those first recorded in the most recent census (1994) to those that were already established at the time of the 1988 census.

For the purpose of this study 12 intervals were classified as 'colonization' sites, or locations that had only been occupied by *S. alba* recently. The following criteria were used in identifying an interval as a colonization site. The site had to have been occupied no earlier than 1991; 7 were first occupied in 1993 or 1994. Because this species can live for several years most of the individuals sampled were likely to be the original colonists or their immediate offspring. In addition, the colonization site had to have been separated by at least one interval from the nearest longer lived population (most were considerably more isolated). This was to ensure that the occupation was not simply the result of spreading of an existing population across the arbitrary interval boundaries. Finally, a minimum of five plants (including at least one of each sex) was required at the time of sampling. At the time of the sampling, new populations consisted of between five and 20 individuals. Analysis of the histories of populations had shown that populations involving fewer individuals rarely grow in number or persist for more than a few years (Antonovics *et al.*, 1994). The number of colonists/site ( $k$ ) was estimated as the number of plants seen at a site the first time it was noted as occupied.

Eleven intervals that had been occupied by *S. alba* continuously since first censused in 1988 were treated as the sites of established populations. Ten of these were sampled in 1993 as reported in McCauley (1994); an additional population was sampled in 1994 to ensure that the colonization sites and established populations were distributed across the approximately 25 × 25 km census area in a roughly equivalent fashion. The sizes of these established populations ranged from 20 to more than 200 individuals.

Leaf material was collected from each individual found within a colonization site and from 20–50 of the individuals found in each of the older populations. The leaf material was used for both allozyme and cpDNA analysis. Methods are described in more detail in McCauley (1994) and will be outlined briefly here. Seven polymorphic allozymes, phosphoglucomutase (PGM, EC 5.4.2.2), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), shikimate 5-dehydrogenase (SKDH, EC 1.1.1.25), isocitrate dehydrogenase (IDH, EC 1.1.1.42), phosphogluco-

nate dehydrogenase (6-PGD, EC 1.1.1.44), malate dehydrogenase (MDH, EC 1.1.1.37), and leucyl aminopeptidase (LAP, EC 3.4.11.1) were scored by subjecting an extraction from fresh leaf material to electrophoresis on starch or cellulose acetate gels. Standards were run on each gel to ensure consistency in allelic scoring. For purposes of statistical analysis a total of 26 alleles was scored; some binning of nearly co-migrating alleles was required. Genomic DNA was also extracted from the leaf material by the method of Doyle & Doyle (1987). Aliquots of these DNA samples were then used as templates in a polymerase chain reaction (PCR) that used primers described by Taberlet *et al.* (1991). These primers were designed to anneal to transfer RNA genes in the chloroplast genome, with the primer sites flanking noncoding regions likely to be variable. Previous work (McCauley, 1994) had identified two insertion/deletion sites within the approximately 1.1 kb region that was amplified by PCR. Four cpDNA haplotypes were recognized by ethidium bromide staining of 4 per cent agarose gels. These four haplotypes were designated as +/+, +/-, -/+ and -/-, where + and - refer to the presence of an insertion or deletion at each site.

Allozyme allele and genotype frequencies, as well as cpDNA haplotype frequencies, were calculated separately for all 23 populations and used to calculate Wright's measure of the among-population component of genetic variance,  $F_{ST}$ , separately for the 12 new ( $F_{ST0}$ ) and 11 older ( $F_{STc}$ ) populations by the methods of Weir (1990).  $F_{ST}$  was first calculated separately for each allozyme locus and for the cpDNA. Information was also combined across allozyme loci in order to provide summary estimates of  $F_{ST}$  based on all protein variants. Statistical procedures used to compare  $F_{ST0}$  and  $F_{STc}$  and to estimate  $\phi$  will be described as the results are presented.

## Results

From the census data the number of individuals first seen at each of the 12 new populations can be used to estimate  $k$ , the effective number of colonists. The new populations consisted of between two and 20 individuals when first noted in the roadside census (see Table 1). Recognizing that with variation in the number of colonists the harmonic mean is an appropriate summary statistic (Whitlock & McCauley, 1990),  $k$  is estimated from the roadside census to be 4.21.

**Table 1** Characteristics of 12 local populations of *Silene alba* founded since 1991

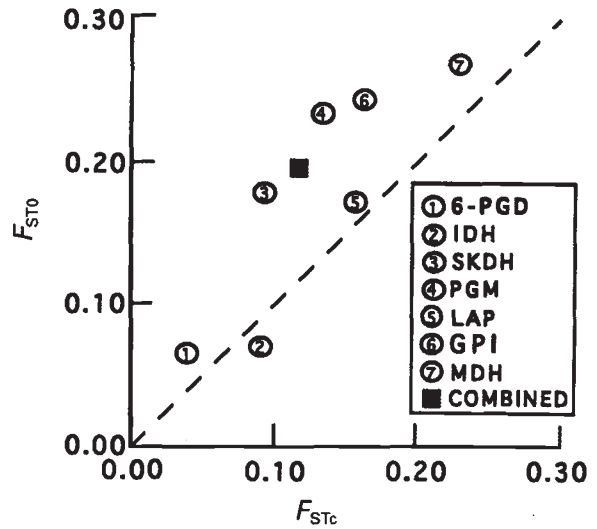
Population	Year first seen	<i>n</i>	<i>n</i> (1994)	Comments
1	1991	2	6	Weedy roadside
2	1991	2	6	Wooded roadside
3	1991	4	9	Wooded roadside
4	1992	3	25	Disturbed roadside
5	1992	15	10	Crevices on rockface
6	1993	9	14	Construction site
7	1993	20	19	Weedy roadside
8	1993	2	7	Weedy roadside
9	1993	4	6	Weedy roadside
10	1994	7	7	Weedy roadside
11	1994	17	17	Horse corral
12	1994	11	11	Wooded roadside

Included is the year each population was first noted in a roadside census, the number of individuals (*n*) present at that time, the size of the population when collected for genetic analysis in 1994, and comments on local ecological conditions.

$F_{ST}$  values estimated for the individual allozyme loci and the values combined across loci are presented in Fig. 1. By using the  $F_{ST}$  values combined across loci (0.197 and 0.126 for  $F_{ST0}$  and  $F_{STc}$ , respectively) and the estimate of *k* provided above,  $\phi$  can be solved from eqn 2. The estimate of  $\phi$  based on allozymes is 0.73.

Single cpDNA haplotypes were found in seven of 12 new populations and five of 11 old populations, the other populations containing two to four haplotypes. This distribution of cpDNA haplotypes resulted in  $F_{ST}$  estimates of  $0.655 \pm 0.12$  and  $0.613 \pm 0.15$  for the new and older populations, respectively. Standard errors were estimated by jackknifing across populations. By using 0.655 and 0.613 for  $F_{ST0}$  and  $F_{STc}$ , and substituting  $1/k$  for  $1/2k$  in eqn 2 to account for the haploid nature of organelle DNA, the estimate of  $\phi$  based on cpDNA is 0.89.

The  $F_{ST}$  values based on the allozymes were analysed further as follows. Three observations are relevant to the analysis. First, the  $F_{ST}$  values for the newly colonized populations are greater than those of the established populations for six of seven loci. The one locus that is the exception, *IDH*, is the most weakly polymorphic of the seven. Secondly, there is considerable locus-to-locus variation in the estimates, with locus-specific  $F_{ST}$  estimates ranging from 0.27 to 0.06 in the new populations and from 0.23 to 0.04 in the older populations. Finally, there appears to be some correspondence between the population age classes with regard to these locus-to-locus differ-



**Fig. 1**  $F_{ST}$  values estimated for 12 recently colonized ( $F_{ST0}$ ) and 11 established ( $F_{STc}$ ) populations of *Silene alba* from allele frequencies at seven polymorphic allozyme loci, as well as an estimate combined across loci. Note that  $F_{ST0}$  is larger than  $F_{STc}$  at six of seven loci.

ences (e.g. *6-PGD* has the lowest and *MDH* the highest value in each case). This would be expected from eqn 2 if the locus-to-locus  $F_{ST}$  differences were real, and if  $\phi$  approached one as estimated above.

These observations prompted the following analysis. The  $F_{ST}$  estimates were arrayed as a two-factor ANOVA without replication. One factor contrasted the age of populations as a fixed effect treatment. The other factor treated loci as random blocks. This design has the advantage of assigning much of the locus-to-locus variation to a block effect, rather than as error variance, thus increasing the power of the age contrast (Sokal & Rohlf, 1981). Further, it allows for a tentative test of the significance of the locus effects, though care must be taken in the interpretation of block effects in this design (Sokal & Rohlf, 1981). The results of the analysis (Table 2) show that the age effect is statistically significant ( $0.05 > P > 0.025$ ). Considering all allozyme loci together, the new populations have a higher  $F_{ST}$  than the older populations. The block effect is also significant ( $P < 0.01$ ), demonstrating a correspondence between established and recently colonized populations with regard to locus-to-locus differences in  $F_{ST}$ .

**Discussion**

There is a long tradition in population genetics of estimating levels of gene flow indirectly from the

**Table 2** Unreplicated two-factor analysis of variance of  $F_{ST}$  values

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>
Age	1	0.007	0.007	7.60	0.025 < <i>P</i> < 0.05
Locus	6	0.056	0.009	10.64	0.005 < <i>P</i> < 0.01
Error	6	0.005	0.001	—	—

One factor is the age of the populations on which the  $F_{ST}$  estimates are based, and the other is the allozyme locus on which they are based.

distribution of genetic polymorphism within and among populations (Slatkin, 1985). Often this assumes that populations are stable entities and in genetic equilibrium, as populations are rarely sampled with regard to history. Recently, however, several authors have studied the impact of local extinction and recolonization on the genetic structure of animal metapopulations using another indirect approach; that is, by comparing the genetic compositions of recently founded and more established demes (Whitlock, 1992; Dybdahl, 1994). The study of *S. alba* reported here represents one of the first attempts to use this second indirect method to study the mechanisms of colonization underlying the genetic structure of a plant metapopulation.

One result of this study is the demonstration that a set of recently founded populations of *S. alba* displays considerable genetic structure and that this structure can be ascribed to a mode of colonization in which there is only limited mixing of individuals from diverse sources. From eqn 2 it can be seen that if colonists were drawn as individuals and at random from throughout the study area ( $\phi = 0$ )  $F_{ST0}$  values would be expected to be considerably smaller than the observed values (0.119 and 0.238 for allozymes and cpDNA respectively, given  $\phi = 0$  and  $k = 4.21$ ). Thus, it is both the relatively small numbers of individuals that comprise colonizing groups and the way in which they are drawn from the metapopulation that generates the genetic structure. Note that the 0.197  $F_{ST0}$  value estimated from allozymes is very similar to the average  $F_{ST}$  values reported in a literature survey by Hamrick & Godt (1990) when that average was based on numerous studies of plant species that were either animal-pollinated outcrossers (0.197) or short-lived herbaceous perennials (0.213). Most of the studies compiled in that literature survey, however, were conducted over a much larger portion of their respective species' ranges and did not distinguish the age of populations.

What ecological factors might limit the mixing of individuals from diverse sources during colonization? One simple explanation is that the colonists involved in a given founding event are drawn primarily from just the nearest source populations. There is support for this hypothesis in a previous analysis of the roadside census data (Antonovics *et al.*, 1994). Most recorded colonization events occur in proximity to established populations. There are also several mechanisms by which groups of individuals could move longer distances together. One is the transportation of soil samples containing ungerminated seeds, either as roadside fill or during construction projects. Another is the movement of clusters of whole plants, as during mowing operations. Finally, it is possible that most colonization events do not involve movement *per se* but rather *in situ* recruitment from a seed bank. Because all colonization sites were known to be empty for the 3–6 years prior to the colonization event, such a seed bank would have to be fairly long-lived. While little is known about seed banks in *S. alba*, there is evidence that ungerminated seeds can remain viable in the soil for at least a year (Peroni & Armstrong, 1994).

Whitlock & McCauley (1990) showed that  $F_{ST0}$  can be increased by kin-structured colonization; that is, when relatives rather than random individuals are drawn from the same source population. Since a *S. alba* female can produce numerous seed capsules, each containing hundreds of seeds, colonization by sib groups is theoretically possible should single capsules or individual plants be the unit of dispersal, as might be the case after mowing. In fact, the  $F_{ST0}$  estimate based on all allozymes (0.197) is very close to that expected when populations are founded by groups which consist of a mixture of full- and half-sibs (Wade, 1982). The likelihood that populations are commonly derived from single sib groups can be evaluated by the analysis of the cpDNA. When cpDNA is maternally inherited, as in *S. alba* (McCauley, 1994), the  $F_{ST0}$  based on cpDNA polymorphism is more sensitive than that based on nuclear genes to the number of maternal lineages involved in founding events (McCauley, 1995). That the observed estimate of  $\phi$  based on cpDNA is higher than that based on allozymes suggests some kin-structured movement. However,  $F_{ST0}$  for cpDNA would be expected to be one if populations were always founded by single sib groups. The fact that more than one-third of the newly founded populations were polymorphic for cpDNA haplotypes shows that founding by a single maternal lineage must not be a pervasive mode of colonization.

(Note that even some of the monomorphic demes may have been founded by several maternal lineages that happened to carry the same cpDNA haplotype.)

The second major result of this study is that the recently founded demes display a larger  $F_{ST}$  value than do the older demes taken from the same metapopulation, at least for the allozymes. This observation is significant for understanding how metapopulation dynamics can influence genetic structure. In a metapopulation with a continual extinction and replacement of demes, an age structure will develop at the level of demes (Wade & McCauley, 1988). If the dynamics of demes of *S. alba* approximates those assumed in the models then the old and newer populations studied here could be viewed as samples from different portions of that age distribution. The smaller  $F_{ST}$  value in the older populations suggests that some evolutionary pressure causes demes to converge in gene frequency in the generations following their establishment.

This convergence would be expected if there were a high rate of gene flow between established populations. An apparently contradictory condition, limited movement leading to colonization (small  $k$ ) and frequent movement between established populations (higher  $Nm$  or gene flow), may be common in plant metapopulations. This is because movement associated with colonization is partially decoupled from gene flow between established populations, because colonization requires the movement of seeds, but (in nuclear genes, at least) the more standard form of gene flow can result from the movement of either seeds or pollen. *S. alba* is insect-pollinated and is likely to undergo considerable gene flow via pollen movement. McCauley *et al.* (unpublished) have shown that target females can be fertilized at distances of up to 640 m from pollen sources. Also, in the previous study of established populations, McCauley (1994) ascribed the fivefold greater  $F_{ST}$  value seen in cpDNA, when compared to allozymes, to the fact that the maternally inherited marker could not undergo gene flow via pollen movement, whereas pollen movement had a substantial impact on the structure of the nuclear markers.

A second converging evolutionary force could be some form of balancing selection acting on one or more of the allozyme loci (Karl & Avise, 1992). The observation of locus-specific differences in  $F_{ST}$  values, such as seen here, has been suggested as an indication of selection (Slatkin, 1987). In any event, in the absence of extinction/recolonization any converging force, be it selection or gene flow, would eventually erode genetic structure. With metapopulation dynamics, such as seen in *S. alba*, how-

ever, that structure is constantly renewed by the recurrent founding events.

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