

Quantitative Genetics in Natural Populations: Means of Monitoring Natural Biological Processes

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Abstract: One of the goals of conservation biology is to maintain the integrity of natural processes in populations of rare plants. In the short term one of the main concerns is often whether the mating system of rare plants is disrupted, for example, by fragmentation. In the long term one of the main concerns is often whether small isolated populations maintain enough genetic variation to respond to selection due to human-induced environmental changes. Management of rare plant populations would, therefore, be supported by tools enabling the effective monitoring of these and similar processes. Unfortunately, direct measures are often difficult, time consuming, or expensive to obtain and therefore not useful for monitoring efforts. We are developing some simple genetic-based methods for quantifying both mating systems and the expected response to selection. They rely on joint genetic and phenotypic data obtained from field-collected samples and obviate the need for intensive breeding designs and common gardens that typify quantitative genetic studies. As a result, they will be directly applicable to monitoring populations of rare plants, and will enable better efforts directed toward maintaining the integrity of natural resources.

The practice of conservation biology often focuses attention on the numbers of individuals present in populations. This is particularly true of most listing efforts, which trigger concern when the number of individuals or populations has fallen to a low level (Wilcove et al. 1993); it is also characteristic of much monitoring effort, which typically seeks to quantify through time the number or density of individuals or populations. This focus on population size results in part from the view that genetic information is at best only indirectly useful in assessing a population (Lande 1988, Menges 1986, Schemske et al. 1994). Inherent in this focus is the assumption that all individuals are equivalent to each other with regard to fitness and that high-quality status information cannot be obtained through assessing status in ways that do not assume that all individuals are equivalent.

Other areas of conservation biology do, in fact, recognize that all individuals are not equivalent. For example, concern among conservation biologists about inbreeding depression or the ability of small populations to respond to selection are founded on the notion that individuals differ in their genetic composition, which may influence their performance. Further, the focus of conservation genetics is on using differences among individuals to provide information on the geographic or taxonomic partitioning of diversity (Avise and Hamrick 1996). Unfortunately, as emphasized by Lynch (1996), there are neither abundant direct empirical connections between such measures of

genetic diversity and the processes of primary concern—including mating systems, inbreeding depression, and response to selection—nor strong theoretical expectations of such connections. Consequently, many practitioners of conservation biology are disenchanted with genetic information.

Nevertheless, it is clear that to maintain the integrity of rare plant populations, natural processes must be maintained in both the short and long term. One process of direct relevance in the short term is the mating system. If it is disrupted by habitat fragmentation or by changes in pollinator abundance, for example, plant populations may respond in detrimental ways due to enhanced inbreeding or simply lack of mating opportunities. Further, changes in the mating system must precede any numerical changes in population size due to the mating system, because at a minimum they are detectable in a parental generation whereas abundance cannot change until at least the offspring generation if not much later, especially for perennials.

One process of direct relevance to long-term management is the ability of a rare plant population to respond to selection. In a changing environment, such as induced by human activities, persistence is dependent on an ability to either colonize new habitats or evolve in situ; the latter of course depends directly on the genetic basis of adaptive traits. Because of the direct importance of these processes, management of rare plant populations would be enhanced by tools enabling the ef-

fective monitoring of these and similar processes.

Unfortunately, direct measures of plant mating systems are often difficult, time consuming, or expensive to obtain and therefore not useful for monitoring efforts. For example, to directly monitor mating systems requires tracking pollen from a source flower to a fertilized ovule. This can be done in part through the use of dyes applied to anthers, but many colors of dye are required to differentiate among source plants, it is extremely labor intensive in the field, and selection at the fertilization stage is always neglected (Kearns and Inouye 1993). Quantifying the genetic basis of an ecologically important trait is at least as difficult, and typically requires extensive breeding and culturing facilities; it may not even be possible for rare plants of immediate concern.

Clearly, there is a need for methods that enable managers to obtain information on the status of a population that is as closely related as possible to the processes of mating and the ability to respond to selection. The remainder of this paper serves as an introduction to some methods that accomplish this. Of necessity, to focus attention on the importance of applying these methods to assist natural resource management, just an overview of the detailed quantitative genetics is given. It is hoped that the main point—that genetic information can be used effectively in conservation biology—remains clear and that managers interested in pursuing these methods will initiate collaborations to apply them to practical problems of interest.

Quantitative Genetics

Quantitative genetics (Lynch and Walsh 1998) focuses on disentangling the relative importance of genetic factors to determine the phenotype of traits with a complex basis involving both genetic and environmental influences. Essentially, all traits of interest to conservation biologists are of this sort. For example, morphological traits that influence pollinator response likely involve the interaction of many genes and many environmental factors; fitness and life history traits can be regarded as measurable phenotypes influenced by both genetic and environmental factors. Thus, the tools of quantitative genetics are of direct relevance to the problem of assessing the mating system and the response to selection in rare plant populations.

Quantitative genetics is based on the premise that genetically related individuals will exhibit greater phenotypic similarity than unrelated indi-

viduals, and further that a quantitative relationship exists between genetic relatedness and phenotypic similarity (Jacquard 1974).

Relatedness

In the traditional development of quantitative genetics, the relationship between a pair of individuals is described by a set of coefficients, $\Delta = (\Delta_1, \Delta_2, \Delta_3, \dots, \Delta_9)$, each of which represents the probability of the four alleles at a single locus in two diploid individuals sharing a particular pattern of identity by descent (Jacquard 1974). In a large, non-inbred population, only Δ_7 , Δ_8 , and Δ_9 are nonzero; consequently, any pattern of relationship between two individuals can be described by that set of three coefficients. A useful summary of the degree of relationship described in more detail by these three coefficients is the coefficient of coancestry (Jacquard 1974, Lynch and Walsh 1998),

$$\theta = \frac{1}{2} \Delta_7 + \frac{1}{4} \Delta_8,$$

which quantifies the probability that two individuals will produce an inbred offspring were they to mate.

Molecular genetic data provides information on the patterns of identity-in-state, for example, which nucleotide sequence is present at each of the four alleles in the two individuals. The pattern of identity in state is determined by the allele frequencies in the population and by the genetic relatedness of the two individuals:

$$\Pr(S) = \sum_{i=1}^9 \Pr(S|S'_i) \Pr(S'_i) \quad (1)$$

where S is a particular pattern of identity-in-state (e.g., all four alleles are a specific nucleotide sequence), S'_i is a particular pattern of identity-by-descent, and the coefficients of relatedness $\Delta_i = \Pr(S'_i)$. Equation (1) is the likelihood equation (Edwards 1992) for the Δ_i and can be used to estimate the relatedness between pairs of individuals given information obtainable from genetic markers on their genotypes.

As with any estimator of genetic relatedness, the quality of the estimate depends on the amount of available genetic information. Typically, both the number of loci for which genetic information is available and the number of alleles segregating at those loci have strong influences on the variance of the estimate of relatedness. Table 1 illustrates how these parameters affect the variance in the estimate of relatedness based on equation (1). It is evident that precision of the estimate increases with increasing numbers of either loci or alleles per locus.

Table 1. Dependence of the variance in relatedness (θ) on available genetic information. The variance was obtained from 1000 simulations with the corresponding number of loci, alleles, and type of marker expression under the assumption that the three coefficients of relatedness are equal: $\Delta_7 = \Delta_8 = \Delta_9$. In each case the alleles are assumed to be equally frequent.

Loci	Alleles	Expression	Var (θ)
50	2	Codominant	0.007815
50	16	Codominant	0.001701
500	2	Codominant	0.000863
500	16	Codominant	0.000169
50	2	Dominant	0.005432
500	2	Dominant	0.000515

Another major factor influencing the estimation of relatedness from genetic marker information is the phenotypic expression of the markers on a gel. For example, it is much easier to obtain genetic data from hundreds of loci using molecular technology that detects dominant markers, such as RAPDs (Hadrys et al. 1992, Williams et al. 1993) or AFLPs (Lin and Kuo 1995, Vos et al. 1995), rather than using more traditional techniques such as RFLPs or DNA sequencing. Unfortunately, dominant phenotypic expression also typically reduces the amount of genetic information available for estimating relatedness between individuals (Lynch and Milligan 1994). Table 1 also illustrates the effect of dominance on the variance of relatedness. Again, more as opposed to fewer dominant markers provide a better measure (lower variance) of the degree of relatedness. In this case, there is little if any increase in variance for dominant compared to codominant markers, but this is not likely to be a completely general result because of the inherent loss of information due to dominance (Milligan and McMurphy 1993). However, these results indicate that at least under some conditions, dominant markers may remain useful for estimating relatedness.

Quantitative Genetics

Traditional approaches to quantitative genetics rely on manipulating or otherwise knowing the degree of relatedness between pairs of individuals, measuring the degree of phenotypic similarity, and using mathematical models (Jacquard 1974) to determine the extent to which genetic variation is responsible for variation in the phenotypic trait. Given that relatedness between a pair of individuals can be estimated using molecular marker data, however, it is possible to estimate the extent

of genetic variation from joint marker and phenotypic data, because they are determined by the pattern of relatedness and the degree of genetic variation. Specifically, the joint molecular marker and phenotypic data can be modelled as an extension to equation (1):

$$\Pr(S, Z) = \sum_{i=1}^9 \Pr(S|S'_i) \Pr(Z|S'_i) \Pr(S'_i) \quad (2)$$

where Z represents the phenotypic information, and S and S' are, as before, a particular pattern of identity-in-state and a particular pattern of identity-by-descent. Note that equation (2) is essentially the same as equation (1) with the addition of a term for the phenotype Z . Given the joint marker (S) and phenotypic (Z) data, one can estimate both the relatedness (Δ) and the degree of genetic variation, which is often quantified by the additive genetic variance and appears in equation (2) as a parameter of $\Pr(Z|S'_i)$.

Figure 1 illustrates an example of jointly estimating the additive (V_A) and environmental (V_E) variance components, along with relatedness. Although there is some variation in the estimates, there is no obvious statistical bias. The approach to estimating the genetic basis of a quantitative trait from joint molecular and phenotypic data is feasible.

Applications to Conservation Biology

The previous section briefly outlines methods for addressing quantitative genetics in the field and estimating properties of natural populations that are relevant to conservation biologists. However, the application of these methods may not be transparent from an introduction to the theory.

To monitor mating systems, one must be able to quantify the pattern of relatedness between individuals. Ideally, that quantification would be carried out periodically to provide insight into how the patterns change through time as a result of environmental conditions, pollinator interactions, or human activities. As outlined above, the necessary information consists solely of a collection of genetic marker data (e.g., allozyme- or DNA-based genotypes) for each individual sampled. Ideally, many loci would be studied, but markers exhibiting either codominant or dominant expression are useful, as are mixtures of the two. In many cases, it will only be possible to obtain information on a few codominant loci and many dominant ones. For each pair of individuals sampled, the methods outlined earlier provide estimates of how closely related are they. Conse-

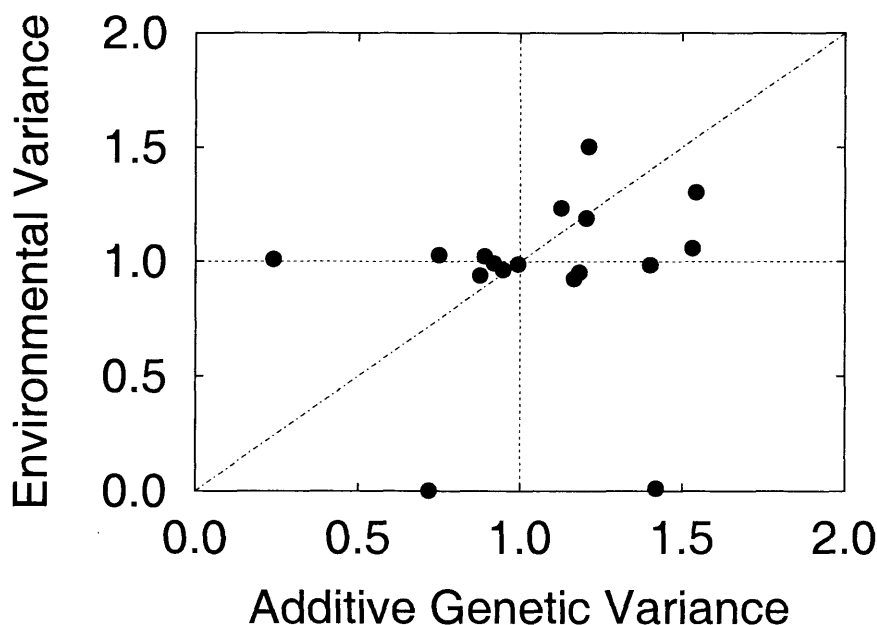


Figure 1. Estimation of variance components. Each point represents the estimate obtained from a single replicate simulation under the assumption of $V_A = V_E = 1.0$; those two parameter values are signified by the vertical and horizontal dotted lines. The dashed line represents values of the variance components corresponding to heritability = $h^2 = \frac{V_A}{V_A + V_E} = 0.5$.

quently, a large sample of individuals provides a picture of the distribution of pairwise relatedness found in the population at the time it was sampled. Comparisons of such distributions across a temporal sequence of samples provides information on such things as whether the mean relatedness is increasing as might be expected in a small, inbreeding population, or whether the variation is expanding as might be expected if some individuals are able to attract pollinators from distant pollen sources and the remainder largely mate with nearby relatives or self. Such knowledge can provide an early indication of biological effects that later could influence persistence.

To monitor the ability of a population to respond to selection, one must be able to quantify the components of variance contributing to phenotypic variation among individuals. In the simplest case, this involves disentangling the additive genetic (V_A) from the environmental (V_E) variance for each trait of interest. Again, this quantification would ideally be carried out periodically to identify changes in the genetic basis of important traits such as fitness, floral morphology, or drought tolerance. In addition to the genetic marker data described above, measurements of each relevant phenotype must be obtained for each individual.

The joint marker-phenotype data yield estimates of both relatedness and the variance components. Comparisons of the variance components across a temporal sequence of samples provides information on such things as whether the additive genetic component, which determines the response to selection (Lynch and Walsh 1998), is declining as might be expected in small populations losing genetic variation. As with knowing how relatedness changes through time, this knowledge of how genetic variation for adaptive traits changes can provide an early indication of biological effects that will increase in importance through time.

Discussion

Although the direct relationship between molecular marker data (e.g., allozyme diversity, RFLPs, or DNA sequences) and factors that affect risk of extinction for plant populations is unclear (Lynch 1996), quantitative genetics approaches can provide more direct measures of risk factors such as changing mating systems or reduced ability to respond to selection.

To take advantage of the approaches to conservation genetics outlined here, studies must be designed to provide both genetic and phenotypic information. Marker data alone can be used to

determine the patterns of genetic relatedness, which in turn are important in monitoring mating systems. In conjunction with phenotypic data on the same individuals, however, one can monitor the degree of underlying genetic variation for ecologically important traits. These traits include the fitness components themselves, as well as morphological traits that influence pollinator interactions or physiological traits that determine growth rates, drought stress, or disease resistance. Thus, it is important for managers to become aware of these possibilities and design their research appropriately.

A number of benefits arise from monitoring biological processes through the use of quantitative genetics. The most significant of these is that the processes being monitored are of direct importance to rare plant populations. For example, by monitoring patterns of relatedness between individuals one may detect the effects of fragmentation or altered pollinator fauna, which affect mating patterns. Effects on the mating system will undoubtedly be detectable long before the population has changed in size or otherwise responded in a way that is visible by non-genetic means.

Another example is that, by including quantitative genetics within a monitoring program, one may be able to track the ability of a plant population to respond to selection. This is particularly critical because the persistence of rare plant populations necessarily involves one of two options: colonize new habitats or evolve in situ. By estimating such quantities as additive genetic variance, one can ascertain whether or not the second option remains viable as a long-term persistence mechanism. One could also determine whether ex situ preservation efforts maintained, for example, by botanical gardens or germplasm storage facilities are reducing an accession's ability to adapt when it is reestablished in natural habitat.

One very large advantage of the quantitative genetics approaches introduced here is that they can be applied to natural, unmanipulated field situations. The estimates obtained apply directly to the population under study and there is no need to manipulate the mating system of individuals. These features are particularly attractive for studies of rare plants, because it is often impossible for either management or ethical reasons to manipulate them to the extent typically required by traditional quantitative genetics.

At the very least, this paper illustrates that it is possible to quantify, in natural populations, bio-

logically important processes of relevance to conservation biology. By expanding the scope of monitoring to consider the fact that all individuals within a population are not equivalent, and to use that as a source of important information, one gains the ability to detect changes long before they might otherwise be visible. Even though the tools of quantitative genetics may be complex to the uninitiated, they can provide an excellent means of using genetic data to enhance understanding and management.

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