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EVOLUTIONARY POTENTIAL IN ORCHIDS: PATTERNS AND STRATEGIES FOR CONSERVATION

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Abstract. Strategies for species conservation should be based on at least two perspectives. First, one should know the demographic health of component populations which includes their growth, decline and interdependence. The second perspective, which I address here, is the maintenance of evolutionary potential, i.e., the ability to respond to change. This potential depends not only on patterns of variation but also on how populations differentiate. One model of evolutionary potential and differentiation in orchids is based on small population dynamics and repeated founder events. Species that show high levels of genetic variation within populations but little among them represent the pool of possibilities for future founding events which generate small populations. When variation is highest among populations, the potential for speciation is very high because populations are already differentiated to some degree, gene flow is minimal, and episodes of genetic drift and natural selection may be common. Conservation strategies can be very different for the two extreme patterns. For high variation within populations and little among them, the focus should be on conserving many individuals and this could be accomplished at one or few populations without substantial loss of genetic resources. When variation is greatest among populations then one must conserve as many viable populations as possible. Patterns of genetic variation can be revealed by molecular methods as well as standard morphometric techniques. Thus, the tools for estimating genetic resources are available to all and interpretation of the results are possible within existing theoretical frameworks.

Fundamental issues of biological conservation are what to conserve and how to do it. One concept that has permeated throughout the diverse field and into the realm of ecopolitics is "the conservation of genetic resources." The idea is not new nor was it intended to be restrictive (Frankel & Bennett 1970), but it has gradually expanded from cultivated plants to forest resources and now to all taxa and levels of organization (Frankel *et al.* 1995) largely due to the realization that all species, no matter how seemingly insignificant, may have a profitability potential (cure for cancer!).

Genetic resources are anything that contains functioning RNA and DNA (thereby excluding shampoos and hair rinses). Genetic resources are genes, organisms, and groups of organisms such as populations, species, and higher taxa. They can also be viewed as ecologically interacting groups of species such as guilds and communities. Which of these resources should be targeted for conservation? Species are usually the focus and I shall argue that for species-targeted efforts, population characteristics will guide the choice of management strategies.

Criteria for Conservation of Species

How do we identify orchid species worthy of concerted conservation effort? Although endangered or threatened species are the most dramatic cases, they are not the only taxa that should be targeted for conservation. Frankel *et al.* (1995) point out that species should be prominent in conservation planning when they are (1) directly harvested or grazed in the wild (timber, medicinal plants, spices, ornamentals, food or forage); (2) used as sources for propagating material (forage plants, wild relatives of crops, ornamentals); (3) crucial for the well being of an ecosystem (dominant or keystone species or otherwise crucial for the survival of other species that are of major concern); or (4) when designated as endangered. Orchids could fit into any one of these categories (except perhaps under the dominant or keystone species criterion).

When I last addressed the subject of orchid conservation more than ten years ago (Ackerman 1987), I focused on the extrinsic and demographic factors that should affect orchid conservation strategies. If one did not conserve the habitat and mutualists of an orchid population (e.g., mycorrhizal symbionts, pollinators), then one would be in danger of conserving the living dead (Janzen 1986). It is clearly insufficient to save a species without saving its biology (e.g., Cropper & Calder 1990). A rough indicator of the status of a species and its mutualists is the demographic health of its component populations. Individuals are immaterial except how their survival and reproduction affect population-level processes. Thus, populations are the basic unit of species conservation.

Minimum Viable Population

Species become candidates for conservation under the endangered or threatened categories when we perceive that their populations are at or below some minimum size for long-term survival—a minimum viable population (MVP) size. MVP is crucial to conservation planning and may be defined as the minimum conditions for the long-term persistence and adaptation of a species or population in a given place (Soulé 1987). There are other definitions of MVP (Frankel 1975, Schaffer 1981, Nunney & Campbell 1993), but all have several features in common. First, MVPs are ecological and apply to particular habitats for a specific time period. They also attempt to incorporate genetic variation and microevolutionary processes such as genetic drift, mating system, gene flow and natural selection, all of which may affect the probability of extinction. These factors are further influenced by random events including natural catastrophes, both biotic (e.g., disease outbreaks) and abiotic (e.g., volcanic eruptions, hurricanes, and droughts).

With a demographic as well as an evolutionary component, MVP assessment is not a simple matter. Long-term persistence or survival of populations under natural or managed conditions are detected through population censuses, projectories of population health, extinction and replacement. The problems and procedures to obtain these data are relatively unambiguous, but answers may take many years of work to reveal (e.g., Menges 1990, Tamm 1991, Waite & Hutchings 1991, Gill 1996).

While the demographic component of MVP is straightforward though potentially complex, the evolutionary end of MVP, adaptation to changing environments, is without a doubt a tricky proposition. How does one characterize evolutionary potential and what does one do to conserve it? In the following sections I discuss the evolutionary potential of orchids and relate it to a model of evolutionary diversification. I shall comment on the relationship between this potential and rates of evolutionary change under contrasting conditions of large and small population sizes. Finally, I propose strategies for conservation of the evolutionary potential of orchids.

Evolutionary Potential of Orchids

The Orchidaceae is one of the most species rich families of flowering plants, perhaps the largest family of them all. Although some have estimated that there are 30,000 species (Garay 1960, Madison 1977), most recent accounts place the number closer to 20,000 (Atwood 1986, IUCN/SSC Orchid Specialist Group 1996). Regardless of exactly how many species there are, the orchid family is a major component of the world's flowering plant diversity, at least in terms of the number of species. By the species richness criterion, the evolutionary potential (and genetic resources) of the orchid family are quite high.

Species richness in the Orchidaceae is often attributed to the plethora of pollination mechanisms that have evolved in response to selection for cross-pollination fueled by the disadvantages of inbreeding. Darwin's (1885) monograph on orchid pollination demonstrated the prevalence of adaptations to enhance cross-pollination. A tradition was established and since then most studies have emphasized mechanisms and "fit" of orchid flowers to their pollinators (van der Pijl & Dodson 1966). The marvels of orchid pollination continue to pour into scientific journals (e.g., Vogel 1978, Ackerman 1983, Stoutamire 1983, Kjellsson *et al.* 1985, Atwood 1985, Dafni & Calder 1987, Peakall 1989, Steiner 1989, Johnson 1995); however, such adaptations are the consequences, not the causes of evolution. Because all families of flowering plants have adaptations associated with the enhancement of cross pollination, such adaptations cannot explain why some families are more diverse than others. We need other criteria to explain why families such as the Orchidaceae, are more species-rich than others.

I propose that we draw our attention to populations because all changes in species and higher taxa are a consequence of accumulated changes within populations. Evolution can only occur if there is variation, and in the case of orchids, it is usually assumed that diversity is a consequence of natural selection playing on this variation. Variation, then, represents evolutionary potential.

We expect that selection for cross-pollination would result in populations with a great deal of genetic diversity. Assessments of genetic diversity in orchid species are scarce (about 1 in 2,000 species), but we do know that in outbreeding orchids, the levels of variation based on the number of alleles per locus and different measures of heterozygosity are usually high (TABLE 1) relative to the average for monocots, short-lived herbaceous perennials, widespread species, tropical species, animal-pollinated outcrossing species, and wind-dispersed species (Hamrick & Godt 1990). However, most of our data come from temperate terrestrial species and these may not be representative of most orchids, tropical and epiphytic.

If we assume that the evolutionary potential of orchids is and has been high, then under what conditions has this variation been enhanced and manipulated, resulting in an extraordinary species diversity with a remarkable array of vegetative and reproductive adaptations? In the following section I outline a model of diversifica-

TABLE 1. Genetic structure of orchid populations. A = Average number of alleles per locus; He = expected mean heterozygosity; Ht = total gene diversity; Hs = average gene diversity within populations; Gst = coefficient of gene differentiation among populations; Nm(S) = gene flow estimates (number of migrants per generation) based on Slatkin's private allele model; Nm(W) = gene flow estimate based on Wright's statistics.

Species	Reference	A	He	Ht	Hs	Gst	Nm(S)	Nm(W)
Orchis morio	Rossi et al. 1992	1.7	0.12	0.13	0.12	0.05		
Orchis longicornu	Corrias et al. 1991	1.9	0.16	0.23	0.22	0.02	4.2	3.7
Caladenia tentactula	Peakall & Beattie 1996					0.03[1]		
Caladenia gemmata	Peakall 1988					0.03		
Drakea glyptodon	Peakall 1988					0.09		
Lepanthes rubripetala	Tremblay 1996			0.40	0.29	0.31	0.48	0.75
Lepanthes rupestris	Tremblay & Ackerman unpubl.					0.17	1.15	1.84
Lepanthes eltoroensis	Tremblay & Ackerman unpubl.					0.22	1.54	0.89
Leporella fimbriata	Peakall and James 1989			0.47	0.45	0.04		
Microtis parviflora	Peakall and Beattie 1991					0.30		
Tolumnia variegata	Ackerman and Ward unpubl.	3.6	0.2	0.20	0.70	0.09	8.0	2.50

[1] Peakall and Beattie used Weir and Cockerham's ø rather than Gst, but the results are usually equivalent.

tion that should apply in principle to orchids as well as other families of flowering plants.

Model of Orchid Diversification

In principle, large populations of outbreeding species often contain substantial genetic variation so that one population may represent a substantial pool of evolutionary potential for a given species. Large populations, on the other hand, may not be where all that potential is realized. Evolutionary change is expected to be slow except under catastrophic selection. On the other hand, most of the total variation of a species should occur among its constituent populations when these are small. Such populations lack the evolutionary inertia of large ones, and when gene flow is limited, change can occur rapidly through either genetic drift or natural selection. Thus, variation may be substantial in large populations, but rapid evolutionary change occurs in small ones.

The only model of differentiation in the orchid family based on these principles was sketched by Gentry (1982), Gentry and Dodson (1987), Zimmerman and Aide (1989) and further elaborated by Ackerman and Zimmerman (1994). It requires that effective population sizes (roughly the number of successfully reproducing individuals) are small. This size effect is exacerbated in orchids because (1) nearly all species are severely pollination limited (Ackerman 1986), (2) often only a fraction of adults in a population successfully reproduce (Calvo 1990), and (3) seed crops in orchids are often biparental rather than multipaternal. Colonization ability is good but interpopulation gene flow is low. Because of small effective population sizes, new populations may be established by colonizers that are very different from the mean phenotype of the parental population simply by chance (founder effect). These colonization events may be common because orchid habitats are usually ephemeral (e.g., Benzing 1979, Ackerman 1983, Case 1987) and the dust-like seeds of orchids carry a tremendous dispersal potential. With repeated founder events and numerous small populations, the effects of subsequent genetic drift as well as natural selection can be dramatic and effect rapid change, perhaps playing a major role in population differentiation and speciation (e.g., Wright 1931, Mayr 1954, Carson & Templeton 1984). Thus, the common condition of small population size in the orchid family represents a natural laboratory for genetic re-engineering where populations may be subjected to episodes of genetic drift punctuated with bouts of strong selection. The flip side of this scenario is that although small populations may be the laboratory for change, that change can also lead to rapid extinction as well as diversification.

With this model, evolutionary potential may reside in either large or small populations. There are two basic patterns of variation representing endpoints of a spectrum of possibilities. In one, most of the variation occurs within populations. Gene flow between populations is expected to be high so differentiation has not occurred (or is progressing very slowly). The other pattern is when most of the variation is among populations suggesting that populations have differentiated to some degree and gene flow is minimal. What patterns do we see in the Orchid family?

Genetic Structure of Orchid Populations

High levels of phenotypic variation within populations should yield high levels of genetic variation unless intrapopulation environmental heterogeneity and phenotypic plasticity are high. The extraordinarily variable *Tolumnia variegata* is a weedy, obligate out-crosser found in Cuba, Hispaniola, Puerto Rico and the Virgin Islands (Ackerman 1995). Plants are twig epiphytes and average adult life expectancy is only a few years (Meléndez & Ackerman 1993). Recruitment is good even though plants are severely pollination limited and the proportion of individuals successfully reproducing in a population can be very small (Calvo 1993). A multivariate analysis of morphological variation (Ackerman & Galarza-Pérez 1991) demonstrated that Puerto Rican populations, regardless of their phenology (spring or fall flowering), are more similar to each other than to populations in the Dominican Republic or Cuba. Despite unsubstantiated claims to the contrary (Sauleda & Ragan 1996), no combination of characteristics can separate the island populations as distinct taxa. Using electrophoretic techniques to ascertain isozyme variation and to estimate gene flow, we discovered that most allelic variation in *T. variegata* of Puerto Rico and the Dominican Republic occurs within populations (Ackerman & Ward in prep.). Population differentiation was insignificant ($G_{st} = 0.09$; 1 = completely different, 0 = no difference whatsoever), and estimates of gene flow were very high, enough to overwhelm the effects of selection or genetic drift ($Nm(S) = 8$; $Nm(W) = 2.5$). Genetic variation as measured by expected heterozygosity and the effective number of alleles per locus (TABLE 1) was higher than average for monocots, short-lived herbaceous perennials, widespread species, tropical species, animal-pollinated outcrossing species, and wind dispersed species (Hamrick and Godt 1990). From any point of view, *T. variegata* is a very healthy species. Populations are large, gene flow is good, and levels of genetic variation are higher than average. There is considerable evolutionary potential, but because of gene flow, evolutionary change is not likely to occur rapidly (Sabat & Ackerman 1996, Ackerman *et al.* 1997). If for some reason *T. variegata* should become a candidate for conservation action, then an appropriate strategy for maintaining the evolutionary potential of this species (based solely on genetic data) would be to conserve as many individuals as possible. This could be accomplished with one or a few populations without substantial loss of genetic resources.

Is the pattern of population genetic structure found in *T. variegata* common in other orchids? The available data show that genetic variation is high, population differentiation is low and inferred gene flow is substantial (TABLE 1). As in *T. variegata,* one may regard the evolutionary potential of such species as very good, but population change is either very slow or stagnant because gene flow counteracts the effects of local changes through genetic drift or natural selection.

Gene flow among populations potentially occurs through both seed and pollen dispersal. Some orchid pollinators, such as euglossine bees, fly long distances (Janzen 1971, Ackerman & Montalvo 1985) but interpopulation gene flow is most often attributed to dispersal of the dust-like seeds. If gene flow is prevalent among orchid populations, then one must conclude that the evolutionary processes in the family proceed at very slow rates, perhaps even slower than most other groups of flowering plants (Soto Arenas 1996). This, of course, contradicts an axiom of orchidology: the family is actively evolving and doing so at a rapid rate (Dressler 1981, Gentry & Dodson 1987). So, which evolutionary scenario is correct?

The answer is that both are correct. With more than 20,000 species in the Orchidaceae, I expect that the family contains a complete spectrum of evolutionary states, from the hyperactive to the stagnant. Where do we look for indications of evolutionary flux? Interspecific hybridization is a means of generating substantial variation and has been identified as one of the most important means of diversification in flowering plants (e.g., Stebbins 1959, Arnold 1997). Hybrid zones are where we expect to detect evolutionary processes that may or may not lead to speciation (Hewitt 1988, Rieseberg & Wendel 1993). Certain groups of orchids, particularly in Europe (e.g., *Orchis, Dactylorhiza*), are subjected to these processes (e.g., Scacchi *et al.* 1990), but elsewhere purported hybrid populations of orchids are too often ill-documented. Alternatively, we should look at patterns of genetic variation among populations of species complexes and species-rich genera much as Gentry and Dodson (1987) suggested that we look at *Anthurium, Piper* and *Cavendishia* for indications of rapid diversification. In the Orchidaceae, good candidates for such studies might be *Bulbophyllum, Dendrobium, Encyclia, Lepanthes, Maxillaria* and *Oncidium.*

In the first detailed study to examine whether or not the conditions for rapid diversification via founder effects, drift and selection exist, Tremblay (1996) employed dispersion, morphology, demographic and genetic assessments of *Lepanthes* populations in Puerto Rico and discovered that both morphological and genetic variation among populations of *L. rubripetala* were quite high. In three species of *Lepanthes,* most subpopulations (individuals on separate phorophytes) differed significantly for many of the characteristics measured, even when the subpopulations were separated by only a few meters. Genetic differentiation in *L. rubripetala* (the only species studied at the time) was substantially higher (G_{st} = 0.31) than studies of other orchids (TABLE 1). As expected when populations are well-differentiated, estimates of gene flow were low (less than one migrant per generation) using both Slatkin and Wright's estimates (Nm (S) = 0.48; Nm(W) = 0.75). Under these conditions, both drift and natural selection may quickly alter the genetic structure and composition of these populations. Tremblay's data suggest that in this evolutionary plastic genus, a great deal of variation occurs among populations; therefore, the appropriate conservation strategy to preserve the evolutionary potential is to target as many populations as possible. Evolutionary action is in these small subpopulations, rarely connected by gene flow and subjected to genetic drift and local selection. This scenario is not only akin to various models of speciation that employ small effective population sizes (Wright 1931, Mayr 1954, Carson & Templeton 1984) but also to those that emphasize the importance of metapopulations in preserving variation and maximizing rates of evolution (reviewed in Simberloff 1988).

CONCLUSIONS

Biological diversity, genetic resources, or whatever one calls it has a present as well as future context. We need to conserve the evolutionary potential of orchids, not just museum pieces. How do we preserve this potential? I have given two examples, *Tolumnia* and *Lepanthes*—both contain substantial evolutionary potential but their variation is packaged in quite different ways. Conservation strategies that are designed to preserve genetic variation and evolutionary potential would be different for the two groups. As we reveal additional patterns of variation through studies of population genetics, other strategies may be appropriate.

Will time-consuming genetic studies be required for every conservation case? Ideally, we should know as much about biological diversity as possible: what is it, how is it maintained, and what is its future? Detailed studies that cover all facets are usually not too practical because of finances, time, or logistics. Fortunately, there are ways to predict patterns of genetic diversity. For example, knowledge of breeding systems and pollination biology may serve as indicators of genetic diversity not only within populations, but among them as well (Hamrick & Loveless 1989). We also have some indication from our work on *Tolumnia* and *Lepanthes* that patterns of morphological variation mirror patterns of genetic variation (at least for isozymes). If this relationship holds, then one need not have a sophisticated laboratory to make a quick and reasonable assessment of genetic variation.

Clearly, patterns of genetic variation are not all that one needs to know. I have emphasized the importance of genetic variation in the context of maintaining evolutionary potential but conservation is an issue because of ecological and demographic urgency. Genetic variation guides our choices for action, but one needs to consider more immediate factors such as the effective population size, trajectory of population growth or decline, and potential for population recovery.

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