Restoration Biology: A Population Biology Perspective

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Abstract

A major goal of population biologists involved in restoration work is to restore populations to a level that will allow them to persist over the long term within a dynamic landscape and include the ability to undergo adaptive evolutionary change. We discuss five research areas of particular importance to restoration biology that offer potentially unique opportunities to couple basic research with the practical needs of restorationists. The five research areas are: (1) the influence of numbers of individuals and genetic variation in the initial population on population colonization, establishment, growth, and evolutionary potential; (2) the role of local adaptation and life history traits in the success of restored populations; (3) the influence of the spatial arrangement of landscape elements on metapopulation dynamics and population processes such as migration; (4) the effects of genetic drift, gene flow, and selection on population persistence within an often accelerated, successional time frame; and (5) the influence of interspecific interactions on population dynamics and community development. We also provide a sample of practical problems faced by practitioners, each of which encompasses one or more of the research areas discussed, and that may be solved by addressing fundamental research questions.

Introduction

Our understanding of the ecological mechanisms underlying successful habitat restoration is not keeping pace with the societal needs for restoration. An improved understanding of the processes involved in a successful restoration can be gained if we learn from the "field experiment" that underlies every restoration project. However, because of the expense of restoration and its often mandated practice, biologists cannot wait to learn the specific responses of every species within every different restoration site. Instead, we need innovative research to develop a general template that will help us to manage ongoing projects and provide guidance for the design of future restoration efforts. As a step toward addressing this problem, this paper summarizes the results of discussions of the Population Biology Group during the Restoration Ecology Workshop of the National Science Foundation.

The long-term viability and credibility of the practice of restoration depends on an understanding of the basic biological and ecological processes that operate at a site under restoration. Restoration projects span a continuum, from augmentation of populations of single species within relatively intact ecosystems to the building of ecosystems from bare ground. This continuum can provide valuable opportunities for comparing the success of restored populations under different sets of initial conditions. However, ultimate goals vary widely, as do the criteria used in judging whether a restoration is successful (Hobbs & Norton 1996; White & Walker 1997).

The discipline of population biology provides one perspective on what might be considered a successful restoration. Population biology is a marriage of popula-

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tion ecology and population genetics. The field of population ecology examines birth, growth, reproduction, and death within populations and seeks to identify the factors that influence the success and distribution of populations. Population genetics seeks to understand how the genetic composition of populations changes over time, and what factors influence the change. The integration of the theoretical and empirical aspects of these disciplines promotes our understanding of the processes involved in causing evolutionary change, especially adaptive change (Harper 1977; Solbrig 1980). As was so aptly stated by Dobzhansky (1973), "nothing in biology makes sense except in the light of evolution." In essence, the conceptual framework of population biology originates from the theory of organic evolution. This conceptual framework forms the basis of a population biologist's viewpoint that restoration is ultimately successful when populations are restored to a level that allows them to persist as dynamic parts of a metapopulation over the long term within a changing landscape. Restored populations must possess attributes necessary for reproduction, growth, migration, and adaptive evolutionary change.

Restoration provides special research opportunities for population biology. Although there is a wealth of population genetic and demographic theory, there is an empirical gap in testing such theory with species chosen for reasons other than their experimental tractability (i.e., model systems). Research in restorations provides a way to close this empirical gap. We see four major research opportunities for population biologists who use restorations for research. First, restorations are fundamentally a manipulation of biota in the field within habitats already degraded. Restorations thus provide a sanction for population biologists to conduct field experiments, sometimes over large spatial scales, that are otherwise unthinkable for fear of resulting effects on natural populations and communities. For example, the demographic and genetic attributes of populations can be manipulated to examine how these factors influence population growth, or extinction, or both.

Second, restored communities are also often characterized by very dynamic temporal change resulting from colonization events and succession. A common restoration goal is to either accelerate or freeze the process of ecological succession. Some species and populations will be established deliberately by the restoration while others might colonize naturally. Thus, restoration projects provide an opportunity for investigating the role of population dynamics and evolutionary responses in nonequilibrium conditions and their importance in determining patterns of succession. The success of restoration may in part be judged by the re-establishment of successional processes that, in the long term, may be characterized by species that were not part of the initial biotic mix.

Third, research conducted within restorations is likely to involve organisms that are not the conventional "models" for testing ecological and evolutionary theory. The practical necessity of manipulation of a wider array of organisms should help, in the long run, to increase our understanding of the robustness of theoretical predictions, as well as providing a broader appreciation of biodiversity. For example, despite the longstanding interest in the evolutionary biology of colonizing species (Baker & Stebbins 1965; Parsons 1983; Barrett & Husband 1989; Rejmánek 1996), there has been surprisingly little direct testing of hypotheses about colonizing abilities in the field or the genetic consequences of colonization. By its very nature, restoration is characterized by colonization processes.

Finally, successful restorations provide case histories of populations that have persisted despite suboptimal edaphic conditions, herbivore pressures, lack of mutualists, and invasion by non-native species. These case histories, and the potential to design restorations as experiments (Pavlik et al. 1993), provide a challenging opportunity for the biologist who wishes to understand population processes within the realistic context of environmental variation, multispecies interactions, and successional change. Because restorations often occur on degraded or virtually unpopulated sites, research conducted in such sites is relevant to understanding the factors that influence colonization, growth, and distribution of populations within a complex ecological arena. Such empirical data are needed for basic tests of population biology theory. Furthermore, understanding the responses of populations to extreme ecological conditions typified by many restorations will help identify the boundary conditions important for population growth, persistence, adaptation, and interactions. Restoration research should afford a rich payoff for understanding fundamental evolutionary and ecological theory.

During the National Science Foundation (NSF) Workshop, we grappled with our charge of identifying research gaps that could be uniquely addressed in a restoration context and also include the definitive components of quality restoration research. This is, in part, because we kept uncovering population biology research that is needed by practitioners to carry out economically feasible, successful restorations. Other than special opportunities discussed above, there really is no reason why a population biologist would submit a proposal, for example to the NSF, to conduct research within a restoration. However, this slights the opportunity for a marriage between field tests of fundamental population biology theory and restoration practice. Instead, the opportunity should be promoted as a conscionable use of public funds for research with a tangible bonus of improved restoration practice. We echo the premise of the Sustainable Biosphere Initiative put forward by the

Ecological Society of America that as habitats continue to deteriorate and as funding for research is limited, "... the greater are the applied needs, the more important becomes the basic research. If this point is not made clear, narrowly based applications will carry the day" (Lubchenco et al. 1991).

In this paper, we discuss five research areas that were of paramount importance in our discussions during the workshop. Though not exhaustive, these research areas include fundamental questions that have long occupied the field of population biology. All were considered appropriate for pursuit in restorations, address practical problems faced by practitioners, and will provide the bonus of useful information for practitioners of restoration. Research areas 1–2 examine the importance of population size and of the amount and type of genetic variation to population establishment, persistence, and evolutionary potential; 3–4 examine variation in successful establishment, persistence, and migration of populations and how this may be influenced by succession and the organization of landscape elements; and 5 examines the influence of interspecific interactions on the colonization, establishment, migration, and growth of populations in the context of community development. The need to obtain specific autecological knowledge and strategies for species reintroductions, as discussed in several recent volumes (Falk & Holsinger 1991; Bowles & Whelan 1994; Falk, Millar, and Olwell 1996), may be lessened by the formation of general templates produced from the suggested research.

We then present a sample from our varied experiences of practical examples of restoration problems where fundamental research in population biology is obviously needed. Most of the problems are complex and bridge two or more research areas, emphasizing the challenge that restorations present to population biologists.

Interaction and communication between biologists and practitioners of restoration are critical elements of restoration biology. Practitioners posed several questions at the workshop that require results from population level research (Clewell & Rieger 1997), including: (1) How do we establish indigenous plant materials at restoration sites? (2) How do we remove or exclude aggressive weeds, pests, and exotic plants and animals that threaten to arrest development of restored projects? (3) Can we take advantage of mutualistic relationships to accelerate restoration results? (4) How do we know if we are introducing organisms with appropriate gene pools into a restoration site? Such questions, together with the practical examples of restoration problems presented here, point to specific gaps in the understanding of population biology and the need for an integrated conceptual framework to guide research that links practical needs with basic science. *Indeed, if we could answer the questions of restoration practitioners, truly we would understand much about fundamental population processes as they occur in nature.*

Research Areas

Numerous principles important to restoration research and practice stem from the integration of population genetic and ecological theory. Many principles and their links to restoration biology are identical to those in the field of conservation biology because populations of restored and threatened or endangered species have small sizes, and restorations can involve threatened or endangered species. Critical reviews of a wide range of population biology principles important to restoration and conservation practice can be consulted for more detail (Harper 1977; Millar & Libby 1989, 1991; Falk & Holsinger 1991; Guerrant 1992; Ellstrand & Elam 1993; Bowles & Whelan 1994; Handel et al. 1994; Frankham 1995; Falk et al. 1996; Young et al. 1996). For example, the basic genetic considerations important in species reintroductions are described in Millar & Libby (1989), Barrett & Kohn (1991), Fenster & Dudash (1994), and Guerrant (1996), while the concepts important to measuring the vulnerability and success of populations are discussed in Gilpin & Soulé (1986), Pavlik (1994, 1996), and Guerrant (1996). Although the conceptual basis for restoration biology is extant, there is still a need to test many of the predictions generated from basic principles (Barrett & Kohn 1991; Fenster & Dudash 1994; Guerrant 1996).

1. The Influence of Numbers of Individuals and Genetic Variation Represented in the Founding Population on Colonization, Establishment, Growth, and Evolutionary Potential.

Evolution of populations requires genetic variation, and the larger the genetic variance, the greater the potential for adaptive evolutionary change (Falconer 1981; Hartl & Clark 1989). Because restoration usually begins with relatively small populations, the amount of genetic variation represented in the founding population can be critical. In small populations, stochastic changes in size can severely reduce the genetic variation within a population, thus increasing the opportunity for non-adaptive evolution by random genetic drift at the expense of adaptive change by natural selection (Ellstrand & Elam 1993). Reduction in population size and genetic variance is expected to increase the opportunity for inbreeding and subsequent inbreeding depression. Strong inbreeding depression following inbred mating has been shown for most wild species examined and can even occur in plants that undergo habitual selfing (Charlesworth & Charlesworth 1987; Lande et al. 1994; Montalvo 1994). Similarly, if a founding population has low genetic diversity, e.g., if the plant material used to restore a site is collected from few parents or from an inbred stock, this can result in low effective population size, severe inbreeding depression, and a decrease in the adaptive evolutionary potential of the population (Barrett & Kohn 1991).

How much genetic variation exists within a population of a given size and growth rate, and how it changes over time, are thus important to the long-term success of a restoration. The effective population size (N_e) provides an index that relates theoretical models to "real world" populations and can be used to help predict the probability of extinction or evolutionary potential of populations. Given a measured amount of genetic drift or inbreeding, N_e is the number of individuals within an "ideal" population mating at random that would produce the observed amount of drift or inbreeding. Thus, "real world" deviations from the ideal assumptions of genetic theory (e.g., random mating, equal sex ratio, non-overlapping generations, constant population size over generations, and no selection) can be encapsulated as differences between the effective population size and the number of reproductive individuals. Typically, N_e is smaller than the census population size, and it is notoriously difficult to estimate for organisms, such as plants, in which matings are difficult to observe or which reproduce vegetatively (Nunney & Elam 1994). Nonetheless, N_e captures both genetic and demographic population processes, and is a metric for evaluating the potential importance of different types of evolutionary processes in altering gene frequencies within populations. For example, in populations with effective sizes <100, genetic drift may be very important in altering gene frequencies from one generation to the next. In contrast, populations with large effective sizes (e.g., >1000) in theory are little affected by genetic drift, and changes in gene frequencies are more likely the result of selection or gene flow.

In practice, there are relatively few estimates of N_e for plant populations (Nunney & Elam 1994), and plants are the foundation for many restoration projects. Additionally, very little is known about factors that affect N_e in nature. For example, Heywood (1986) has demonstrated that the large differences in reproduction observed among plants within natural populations (i.e., reproductive hierarchies) often reduce effective population size dramatically. Experimental manipulations of both plant density and resource availability have further indicated that potential reductions in effective population size are greatest in dense populations within productive environments (Rice 1990). Because restoration projects often manipulate both plant density and site resource availability, they represent excellent opportunities to increase our understanding of how ecological factors influence N_e. The potential also exists to study the interaction of demographics and genetics on effective population size because the initial demographic and genetic structure can be manipulated in a restoration.

Restorations also provide special opportunities for research linking genetic diversity to population growth. There are few studies that explicitly examine how the persistence and growth of populations vary as a function of their genetic diversity (Leberg 1993; Young et al. 1996). Restored populations can be manipulated in terms of their initial genetic diversity and population size in the field with relative impunity, as pointed out in the introduction. Population growth rates can then be modeled to facilitate an explicit comparison of growth rates of populations having, for example, natural versus reduced genetic diversity. This may entail population vulnerability analysis (PVA *sensu* Gilpin & Soulé 1986) of rates of population growth, stability, or decline (Pavlik 1994; Guerrant 1996). Once a demographic model of population growth is constructed, sensitivity/elasticity analyses of the model can then be used to identify the critical life history stages that make the most important contribution to population growth (Caswell 1989). The explicit link between genetic diversity and population growth rate, which is the comprehensive measure of fitness (Endler 1986), could be made. The results of such experiments could answer practical questions about whether there is a critical minimum population size for population establishment and persistence and whether certain mixes of genotypes accelerate initial population growth. Results of sensitivity/elasticity analyses have value for establishing guidelines for the kind of material (e.g., seeds versus cuttings) to use in restorations.

Currently, restorations represent missed opportunities for explicitly testing the hypothesis that genetic diversity is necessary for population persistence and, if it is, over what time frame. In part this opportunity is missed because it is commonly (although surprisingly to us) argued that genetic diversity is not a critical issue when restoring a habitat. For example, there is the cost of genetic screening. There is a certain reluctance to embrace the issue of genetic diversity when most previous research training and focus have been on ecosystem functioning, e.g., provision of trophic support. There is also the view that environmental considerations, such as water quality for subtidal wetlands, are of larger immediate importance for restoration success. This is certainly true, but research should lead to improved site selection and preparation such that the short-term success of a restoration is less risky to the long-term goals. Improvements in short-term success in turn should enable refocusing on longer-term goals for success.

The academic debate among conservation biologists of the relative importance of demographic considerations of very small population size versus genetic diversity for effective management of threatened species (Lande 1988; Doak 1989; Schemske et al. 1994) has helped fuel the belief that genetic diversity is of secondary importance in restorations. In part this debate exists because of the paucity of empirical data that link genetic diversity to population persistence, including direct tests of the relative importance of small population size, low genetic diversity, and environmental stochasticity. These tests could be performed in restorations (Pavlik et al. 1993). As pointed out recently (Nunney & Campbell 1993; Lande 1994), both genetic diversity and demography offer important insights on how populations persist, grow, and adapt.

In summary, restorations should offer excellent examples for the population biologist of the potential importance of evolutionary processes in ecosystem restoration and sustainability.

2. The Role of Local Adaptation and Life History Traits in the Success of Restoration.

Evidence from a variety of ecological and genetic data supports the view that populations can be locally adapted (Bradshaw 1984; Linhart & Grant 1996). For example, many studies have found correlations between environmental variables and phenotypic variation in both plants and animals (Conkle 1973; for review see Endler 1986). Given that plants of the same genotype can differ phenotypically depending on their environment, some of the variation detected could be explained by a plastic response to the environment rather than by heritable variation. Indeed, many researchers have argued that phenotypic plasticity itself is a trait subject to selection (for reviews see Bradshaw 1965; Schlichting & Levin 1986; Via 1987). Research has verified that local adaptation promotes higher fitness under the specific ecological conditions of a site, including metal concentrations and herbivore loads (Clausen et al. 1940, 1947, 1948; Silander 1985; Schmidt & Levin 1985; for reviews see Harper 1977; Bradshaw 1984; Millar & Libby 1989; Huenneke 1991; Linhart & Grant 1996).

For restoration, a critical question involves the source of genetic material with respect to its adaptedness. The large amount of genetic variation in many populations offers restoration ecology an opportunity to closely match locally adapted variants with the proper microsite conditions. Use of proper genotypic variants is becoming a more common concern in restoration planning (Millar & Libby 1991; Fenster & Dudash 1994; Handel et al. 1994; Guerrant 1996). In newly restored ecosystems, the presence of ecologically relevant genetic variation within populations of the few dominant species planted on a site may strongly affect restoration success (Smith & Bradshaw 1979; Bradshaw & McNeilly 1981). Carefully selected restoration sites can be used to test predictions about the performance of suspected locally adapted genotypes (including life history variants) in novel environments. There is also a need to assess whether single or multiple sources of seeds present the best strategy for initiating populations in novel environments, especially in the case of rare species in which genetic variance may already be very low within any single source population (Barrett & Kohn 1991; DeMauro 1994; Guerrant 1996). Identifying the environmental amplitude and plastic responses to novel or extreme habitats (Hoffmann & Parsons 1991) can be a useful bridge between the needs of restoration practitioners and evolutionary biologists.

Physiological variants that are successful under special conditions also can be identified for many species, and used or tested in newly restored sites. For example, variants that tolerate unusual soils, such as those rich in heavy metals, offer special opportunities for population biologists interested in the role of ecotypic variation in the restoration of very degraded sites (Bradshaw & Chadwick 1980).

Locally adapted populations often represent a "genetic memory" shaped by past selective events that, although infrequent (e.g., 50-year freezes or 100-year droughts), are nonetheless important agents of selection. Introductions of non-local genotypes that dominate a population initially, but cannot withstand extreme selective events over the long term, represent a non-sustainable restoration strategy. The gene pool of plants well-adapted to local environments can be swamped through competition with a more poorly adapted gene pool of non-local plants if they outnumber the local plants (i.e., if genetic pollution occurs). In large-scale restoration projects, introduced plant material with often limited genetic variability may be spread over a spatial scale that approaches that of a landscape. As a result, the adaptive capacity of a few genotypes of a particular plant species might determine the success of the restoration of an entire watershed.

"Genetic pollution" may also occur through hybridization of individuals from different gene pools. Even when initial hybrids demonstrate increased fitness relative to the parental population (i.e., heterosis or "hybrid vigor"), subsequent generations may suffer reduced fitness (i.e., outbreeding depression; Wallace 1968; Falconer 1981) and the buildup of a "genetic load." Outbreeding depression has been shown to occur in wild species of plants at both regional and very local levels (Waser 1993; Guerrant 1996). However, there is insufficient evidence for deciding the likelihood that outbreeding depression will occur in the event that non-local gene pools are utilized in restoration (Fenster & Dudash 1994). Within a restoration project, the ability to manipulate the initial genetic "mix" provides at least the possibility for testing questions about the persistence and intensity of genetic loads within populations that represent a mixture of local and non-local genotypes.

The considerable natural variation within and among species in life history traits including life form (annual, perennial), sexual versus asexual reproductive mode, and generation time has long held the attention of evolutionary and population biologists. In plants, life history attributes tend to correlate with colonization ability, mating system, population structure, and population growth rates (Hamrick & Godt 1989; Hamrick et al. 1992) and may provide clues to understanding population colonization, establishment, and subsequent persistence and growth. Given the correlations of such traits with genetic diversity and gene flow potential, problems associated with using non-local germplasm may be greater for plants possessing particular combinations of life history and reproductive traits. Consequently, the potential for their populations to become locally adapted may also vary. New research could determine the effect of using non-local germplasm on population fitness in species that represent a range of life history attributes. This would allow tests of predictions concerning the sensitivity of particular combinations of life history attributes to genetic pollution.

The link between life history attributes and colonization ability is also an important research area. Because natural colonization events are difficult to witness, restorations provide the opportunity to focus on the colonization and establishment phase of population growth. Founding populations can be experimentally manipulated in large field settings. One example of a potential research question is the relative importance of asexual and sexual (seed) reproduction in the survival, growth, and spread of plant populations. This question can be studied under a variety of environments and genetic backgrounds in restorations, allowing an understanding about which life history strategies are favored under particular environments.

3. The Influence of the Spatial Arrangement of Landscape Elements on Metapopulation Dynamics and Population Processes such as Migration and Gene Flow.

The specific position of a restoration within the landscape may influence the fate of a restoration project (Bell et al. 1997). Even when restoration is successful, the restored site may be spatially isolated from other similar habitats. As a result, restored landscapes often are fragmented. Understanding the metapopulation dynamics of restored populations requires information about natural colonization and extinction rates and the degree to which the populations are linked by migration (i.e., gene flow via pollen and seed dispersal; Gilpin 1987; Hastings & Harrison 1994; Fiedler & Laven 1996; Primack 1996). The use of demographic data in transition matrix models to explore metapopulation dynamics has proved valuable in understanding population viability (Menges 1990). However, inclusion of genetic diversity, genetic structure, and gene flow data is needed to better understand metapopulation dynamics and long-term population viability (Hastings & Harrison 1994).

The lack of knowledge concerning the effects of isolation is especially notable for evolutionary processes such as adaptation and gene flow, processes that have long-term effects on the stability and sustainability of populations targeted for restoration. For example, fragmentation of populations can either increase or reduce gene flow (Young et al. 1996). Because gene flow is such a powerful evolutionary force (Slatkin 1985), increased gene flow could drastically alter a species' genetic architecture and disrupt local adaptation, while decreased gene flow and isolation of populations could allow higher rates of genetic drift or selection, depending on the population size (Endler 1977; Slatkin 1973).

Gene flow among fragmented populations and genetically divergent restored populations has become a major concern in the restoration of plant populations (Millar & Libby 1989; Barrett & Kohn 1991; Fenster & Dudash 1994; Knapp & Rice 1994) because of the potential for outbreeding depression and disruption of local adaptation by an increased influx of inappropriate (i.e., maladapted) genetic material. Surprisingly little is known about the effects of human-induced fragmentation on patterns of gene flow (Lacy 1987; Lande & Barrowclough 1987; Robinson & Quinn 1992), but studies on "naturally fragmented" populations of colonizing or weedy species strongly suggest that both the severity and the pattern of fragmentation should have a marked effect on gene flow (Larson et al. 1984; Ellstrand & Marshall 1985; Young et al. 1996). An explicit consideration of the interactions between populations on restored sites and landscape-level elements could significantly improve our understanding of the effects of fragmentation on the demographic and evolutionary dynamics of natural populations.

4. The Effects of Genetic Drift, Gene Flow, and Selection on Population Persistence within a Defined, often Accelerated, Successional Time Frame.

Currently, there is very little information on the relative importance of evolutionary mechanisms of genetic drift, migration, mutation, and selection over successional time. Successional changes at a restoration site provide an excellent opportunity to examine whether evolutionary changes occur in concert with community dynamics. The dynamic nature of successional changes, particularly if accelerated by human manipulation, can be used to examine non-equilibrium dynamics of genetic variation in space.

The limited information available on evolutionary changes during succession suggests that both selection and drift can occur. Along a forest successional gradient, Scheiner & Teeri (1986) examined the potential genetic basis for population differentiation among populations of a perennial grass (*Danthonia spicata*) in response to changes in light availability. Two conclusions are relevant to our discussion. First, the persistence of *D. spicata* along successional light gradients was primarily dependent on phenotypic flexibility (i.e., plasticity) rather than narrowly defined genetic adaptation. Second, the genetic differences that occurred among *D. spicata* populations were more likely the result of genetic drift rather than selection.

Because change in physical and biological conditions is intrinsic to restoration, it may be rewarding to use restoration experiments to examine how genetic drift and selection interact in time to create genetic structure (the non-random distribution of genotypes in space). Experiments could also be done to identify the conditions that determine whether a variety of narrowly adapted genotypes or fewer, but phenotypically plastic, genotypes in the population leads to greater population success.

In restorations, the disturbed habitat might provide a novel environment in which strong selection can occur. However, successful adaptation may not be possible if this coincides with conditions for rapid genetic drift due to the established population having a small effective size. Thus, evolutionary processes might operate at a more rapid temporal scale during restoration, blurring the distinction between "ecological time" and "evolutionary time." From the practical point of view, if degraded sites undergoing restoration provide harsh environmental conditions that translate into extreme selection regimes, then the establishment of vegetative cover can be delayed by the selective elimination of poorly adapted genotypes (McNeilly 1987).

Studies of genetic structure under non-equilibrium conditions would make important contributions to population genetics. After Sewell Wright (1943) proposed that evolution through isolation of populations by distance results in the non-random distribution of genetic variation in space, population geneticists have used his F statistics (Wright 1951) to infer levels of gene flow among populations. However, an underlying assumption relating F statistics to gene flow is that the distribution of genetic variation has reached an equilibrium, i.e., genetic divergence via genetic drift is balanced by migration. Theoretical models indicate several hundred generations can be required before equilibrium is reached. Until then, gene flow is highly dependent on how genetic variation is distributed within and among subpopulations (Varvio et al. 1985). This theory, and also the appropriateness of using equilibrium models such as Wright's F statistics to infer gene flow, could be field-tested in restorations.

Understanding how changes in species interactions influence selection over successional time is a difficult problem. In a study on successional processes in permanent pastures, Aarssen & Turkington (1985*a*) proposed that species associations become more predictable as succession proceeds. In an accompanying paper (Aarssen & Turkington 1985*b*), they further suggested that increased persistence of species associations fosters competitive coevolution whereby competitive abilities become more balanced by reciprocal selection during succession. Experiments that test such predictions could be attempted at restoration sites.

5. The Influence of Interspecific Interactions on Population Establishment, Colonization, Growth, and Community Development.

No population exists in an ecological vacuum, and population biologists need to study the effects of biological interactions on the dynamics of populations. Historically, such research has been restricted to two interacting populations and a limited suite of interactions. Competition, herbivory, predation, parasitism, and mutualisms all play roles in the development and fate of restored sites. Restorations offer an opportunity to expand research on community interactions in a significant way because of the great variation in the "ecological theater" (Hutchinson 1965) surrounding them, which can be small, simple, and distant; or extensive, complex, and next door. Such variation provides a means to test hypotheses about the influence of population size, species diversity, isolation, and the strength of species interactions on population growth and community development. The composition and position of the surrounding biotic matrix will steer the restoration into certain population trajectories, influencing, in turn, the functioning and fate of the restored sites. The interplay between the restored and surrounding populations offers much opportunity to understand the fate of colonizing or new populations, especially those that appear at the edge of a range.

Because restoration sites are prone to invasions by non-native species, and because the history of the site is usually documented, restorations provide opportunities to investigate the ecological effects of non-native species on native communities. The ecological effects of non-native species on native communities are very poorly known, as pointed out in a Special Features issue of the Ecological Society of America ("Advances in Invasion Ecology," *Ecology*, Volume 77 (6), 1996). Competitive exclusion of desirable natives by weedy exotics can threaten the success of restorations, especially on highly degraded sites. In some restorations invaded by non-native species, the ecological interactions are painfully evident (see below—the practical example of invasive species in Hawaii), and the economic impetus to study them is great. In other cases, ecological interactions are less apparent. For example, expensive eelgrass restorations were reputed to fail in San Diego Bay due to invasion by the non-native mussel *Musculista senhousia*. In natural unfragmented eelgrass populations, mussel populations declined, while in the fragmented, sparse eelgrass transplanted populations, the mussels interfered with eelgrass vegetative propagation (T. Reusch & S. Williams, unpublished data). The ecological interactions were much more complex than was suggested by a negative correlation between eelgrass and mussel abundances, and could be dissected only by using both restored and natural habitats.

Mutualistic interactions play a pivotal role in population establishment, reproduction, migration, and community development. The importance of mutualists, ranging from bacteria and mycorrhizae to vertebrate seed dispersers, in the ecological functioning of communities and whole ecosystems has become an important part of ecological research (Boucher 1985; Allen 1991), and restored populations offer opportunities to address key interactions (Handel et al. 1994; Handel 1997).

Restoration of plant populations is a necessary, but not sufficient, action to rebuild a functioning habit. For most plant species, interactions with mutualists such as pollinators and seed dispersers are needed for the sustainable growth and population increase of species of interest. Unfortunately, for mutualists such as bees and other pollinating animals that may act as keystone community members of natural and modified environments, we usually know little or nothing about their relative species abundances and diversity. For example, the biology of thousands of species of native bee pollinators is poorly known, and many bee species themselves are threatened and in need of population enhancement (Buchmann & Nabhan 1996). Also, there is a greater diversity among pollinators and dispersers in their foraging and movement patterns and their effects on reproductive success and gene flow of plants (Beattie 1985; Seeley 1985; Roubik 1989; McClanahan & Wolfe 1993; Robinson & Handel 1993; Willson 1993; Buchmann & Nabhan 1996).

Understanding the roles of population size, dispersion, and distribution among habitat types is critical to understanding the strength of population interactions. Restored populations, engineered at different sizes and in different settings, give ecologists the opportunity to understand the thresholds of population size that determine maximum efficiency of dispersal and recruitment for interacting populations. For example, the limiting resource for a mutualist can be identified through experimentation in restorations where the initial matrix of interacting populations and their sizes are controlled. For bee species, holes for nest initiation rather than nectar and pollen might be limiting. The provision of artificial substrata for nesting in restorations enables manipulation of population densities (Roubik 1989; Buchmann & Nabhan 1996). Information about the population sizes, resource requirements, movements, colonization, and foraging patterns of mutualists will inform us about potential for the evolution of specialist interactions and whether restored plant populations reproduce compared to merely surviving in a proper microsite.

Using restorations for experiments regarding the influence of species interactions on the success of populations can also provide a critically needed bridge between population biology and community ecology. Changes in the structure of communities follow underlying changes in the births and deaths in the interacting populations. Because restorations experimentally manipulate the numbers of individuals and species under at least semi-controlled conditions, they present the opportunity to quantify the underlying demographic changes in interacting populations that fundamentally control community structure. Thus, the study of the regulation of community structure can move from being observational and inferential to becoming more mechanistic and predictive.

The practical payoff for research on species interactions in restorations is great. As many restored sites are financially tied to scarce public funds, links among plants and mutualists must be established early in a restoration project to avoid the need for additional intervention, such as adding new individuals or species, in future years. Presently, there are virtually no commercial sources for many native species of pollinators, and, thus, the restorationist will be dependent upon knowledge of these species in the wild. Furthermore, even if a surrogate pollinator is very effective, the chance that it will disperse pollen in a way similar to that of the natural pollinator may be small. Seed-dispersing mutualists must also be attracted to restoration sites to implement the dual roles of spreading individuals of installed plant species and introducing new ones from surrounding areas. If seed dispersers are abundant around and within a restoration site, then the potential for population growth and gene flow is high, as long as the surrounding area does not provide more favorable habitat (Bronstein 1995).

Many other types of species interactions have important effects on restoration success. Populations of herbivores may move quickly into a small restoration from a large surrounding community and devastate the newly established plant populations. Microbial and other soil mutualists such as mycorrhizae, nitrogen-fixing bacteria, saprophytes, and the many cryptic phyla of animals potentially regulate the growth rate of restored populations. Soil amendments and inoculations may add to the richness of these species, and restorationists must consider the level of soil remediation with these mutualists for population persistence. Reserved soil for seed bank additions has been used for several sites, and these soils also may be quite useful for microbial sources (Leck et al. 1989). From the discussion above, it should be clear that the ecology of these interactions is too poorly known to guide restoration practices.

Practical Examples

The interfaces among the research areas presented above are obvious and are exactly where some of the most challenging research exists. For example, what refinements of evolutionary theory are needed to capture the essence of population dynamics within the complex background of communities and ecosystems changing through time? The restoration problems highlighted in the practical examples below include elements from most of the research areas discussed in the previous section. Some also include other elements, such as the interface of autoecological research and population biology. Our current understanding of population biology is limited, and this becomes clearer when put to the test of restoration practice.

Limited stock selection from donor populations. Lack of genetic diversity within restored populations may accelerate their failure to persist, even in the short term. Seagrass restorations may be one example. Seagrass beds have been targeted for restoration in many coastal areas because they are important to coastal water quality and the ecological functioning of intertidal and subtidal marine environments (Williams & Davis 1996). Seagrass restorations are conducted by removing vegetative material from an adjacent seagrass bed because seed germination and seedling recruitment are very limited in natural populations. A practical problem is that the material is typically collected by SCUBA divers who cannot effectively cover large areas of underwater habitat. Material has been collected from areas as small as 200 m^2 (S. L. Williams personal observation). Because seagrasses are highly clonal, the transplantation stock might represent few clones and only a fraction of the natural genetic diversity of a population. Furthermore, adjacent source beds can be ones that were established previously using similar techniques. Williams & Davis (1996) have shown that the genetic diversity of transplanted eelgrass beds is lower than that of natural untransplanted beds in San Diego County, California. Previously, more attention had been paid to determining the type of seagrass material to establish, the appropriate site characteristics, and the functional equivalency of the created seagrass habitat than to the population-level attributes. Despite this knowledge, most seagrass mitigations have resulted in a net loss of habitat (Fonseca et al. 1988). Given the low genetic diversity and potentially small effective population sizes of the restored seagrass populations, this example points to the need to understand how genetic factors interact with environmental factors in determining the persistence of restored populations.

The use of non-local germplasm. It is the policy of numerous government agencies to follow germplasm transfer guidelines designed to maximize genetic diversity, inbreeding avoidance, and the chance that the germplasm used is appropriately adapted to environmental conditions of the planting site. A combination of population genetic theory, studies on local adaptation in plants, ecological genetic work, and provenance (common garden) tests (Clausen et al. 1940, 1948; Kitzmiller 1990), together with numerous studies of the genetic structure of natural populations of plants (see Hamrick & Godt 1989; Westfall & Conkle 1992), served to steer the creation of guidelines.

Unfortunately, germplasm transfer guidelines for non-tree species are frequently ignored by land managers and practitioners for a variety of logistical, financial, and personal reasons. The genetic background of planting stock used is often non-local or unknown, is often low in genetic diversity, and may even include nursery or field-raised individuals exposed to unintentional selection (Hillyard 1990; A. Montalvo, personal observation). If population biologists and agencies expect to gain the cooperation of practitioners in adhering to germplasm transfer guidelines, it is critical that we test the fundamental building blocks of the guidelines in ways that have direct application to problems faced by practitioners. The information garnered will allow fine-tuning of germplasm transfer guidelines so that practitioners can be better advised about use of guidelines.

The fitness consequences of using non-local germplasm are being examined in coastal sage scrub vegetation. This is one of the most endangered plant communities in North America, primarily because of extensive urban development in the Mediterranean climatic regions of California where it occurs. Within this habitat, frequent wildfires, construction, mitigation, and recreational activities result in continuous restoration and revegetation efforts. After large-scale wildfires, public agencies frequently practice erosion control by seeding burned slopes adjacent to densely populated residential areas. In recent years, mixtures of seeds from native and naturalized species have been used in these revegetation efforts. The genetic background of the seeds was non-local or unknown. Even in habitat restoration work where such urgency is not a factor, managers often resort to using plant sources of unknown genetic or ecological origin (Hillyard 1990; A. Montalvo, personal observation).

Dramatic differences often exist between individuals indigenous to a restored site and those introduced. This is especially true for widely distributed species that exhibit geographic variation in numerous traits. For example, nursery stock of the shrub *Salvia mellifera* Greene (black sage) was transplanted into a pipeline corridor cut through an ecological reserve in southern California. The transplants within the restored zone flower later than the indigeous surrounding population (A. Montalvo, personal observation). Such asynchronous flowering has been found to be detrimental to fitness in other plants. In one experimental study of a tropical shrub in which groups of plants were forced to flower asynchronously with the rest of the population, the smaller, earlier-flowering groups suffered decreased seed-set and increased seed predation compared to the general population (Augspurger 1981). Restoration sites offer an opportunity to examine whether phenological, morphological, or physiological differences affect herbivory, pollinator visitation, fruit initiation, seed set, and seed predation of plants.

Genetic bottlenecks and unwanted selection in commercially produced seeds and plants. Even when local germplasm is used to provide plants for restoration, there is an opportunity for "unconscious selection" when seeds are collected for agronomic "increase" or raising of container plants for outplanting. First, initial seed collections could be from small or depleted natural populations, introducing founder effects. Second, under the unnatural conditions of seed increase and container plant production, it is entirely possible that significant shifts in genotypic frequency may occur in a relatively short time. Evidence from the agronomic literature suggests that significant shifts can occur within a single generation (Stanford et al. 1960). Third, container plant increase often involves rooting of cuttings from a limited number of parental individuals, accentuating the potential for selection of few genotypes that are well adapted to the nursery environment. Factors such as climatic differences, fertilizer application rates, harvesting techniques, and horticultural practices might shift the genetic constitution of a collection in ways that may reduce its potential for successful reintroduction into the original site (Rice 1995). There is a need for examining the hypothetical success of agronomically and horticulturally increased populations in restoration sites relative to the use of more diverse, untreated control populations.

Absence of mutualists. Pollinator specificity is a phenomenon that can significantly complicate restoration efforts. For example, within vernal pool communities in the Central Valley of California, Thorpe and Leong (1995) have shown that many of the endemic annual species found within the pools rely on native, solitary, ground-nesting andrenid bees with high specificity of floral hosts. In addition, these pollinators are characterized by limited flight ability and a tendency to remain near the natal nest, so their ability to colonize new habitats is limited. A study by Leong (1994) on the pollinators within six-year-old artificially constructed vernal pools located 25 km from a natural pool complex provided further evidence for the limited dispersal and colonization ability of these andrenid bees. Although the artificial pools contained suitable host plants and were supplemented by additional potted plants, over two flowering seasons no andrenid bees were observed visiting flowers. Leong (1994) further examined the potential impacts of this lack of andrenid bee pollinators by using potted individuals of the endemic vernal pool annual *Blennosperma nanum* (Hook.) Blake (Asteraceae) as phytometers (living meter sticks) of pollinator effectiveness. Compared to natural vernal pools, the insect visitation rate, number of pollinator taxa, and seed set were significantly lower in the artificial pools. Plants within the artificial pools also exhibited a greater tendency for pollen limitation of seed set. Taken together, these results suggest that successful restoration or creation of vernal pools depends critically on the proximity of natural pools. In general, restoration sites can yield novel opportunities for studying the relative effectiveness of flower visitors as pollinators and the importance of species-specific host–plant mutualisms within sites as well as at a landscape level.

Even when a minimally disturbed or essentially natural habitat appears intact, it can be suffering from what has been called "chemical habitat fragmentation" (Nabhan & Buchmann 1997). One such example of chemically altered habitats occurs on federally protected borderlands between the United States and Mexico. Species of night-blooming cacti (*Peniocereus* spp.) bloom for only 2–3 nights per year and are pollinated at night by hawkmoths in the genera *Hyles* and *Manduca*. The larvae of these moths are the tomato hornworms familiar to gardeners and are heavily sprayed in Mexico. The volant adults are essential to the reproduction of plants on the U.S. side of the border where pesticide drift and overflights endanger the pollination and subsequent reproduction/fruit set of these cacti. This type of subtle chemical pollution and strategies to correct it are important to consider when establishing plant/pollinator populations at restoration sites.

Competition with invasive species. The presence of unwanted invasive species makes restoration a formidable task. Restoring native plant communities in the Hawaiian Islands has been an especially difficult problem because of the density and aggressiveness of alien plant species (Loope & Medeiros 1994). Naturalized alien species account for nearly half (47%) of all flowering plant species in Hawaii (Wagner et al. 1990). Any restoration project in Hawaii must deal with invasive species that are not only alien to the site but probably alien to the island chain. Many restoration projects have been "passive," involving weed eradication and fencing of degraded areas to exclude non-native ungulates in order to allow natural regeneration to occur. Fencing to protect native seedlings, however, can sometimes simultaneously exacerbate the weed problem by eliminating grazing animals (Loope & Medeiros 1994).

Current research examines life history traits of alien woody species in natural areas throughout Hawaii in an attempt to determine what makes these non-native species so successful (Reichard 1996). Herbaceous species have not been assessed in this study, though they are a particular problem in mesic and dry sites. Understanding differences in life histories and environmental requirements of weeds relative to native species is of particular interest to land managers and ecologists who are attempting to restore a site. This research can be used to test and improve theoretical models of plant invasiveness (Rejmánek 1996).

Reintroduction of threatened and endangered plant populations.

Reintroduction of plant populations is a recommended strategy in approximately one-third of the management plans for species listed as threatened or endangered by extinction. Reintroduction is often deemed necessary because natural dispersers are absent, the habitat is fragmented, and local seed production is too low. Although it has been assumed that reintroduction is a viable management strategy, evaluations have uncovered a surprisingly high number of failures. These failures raise questions concerning what is the appropriate life history stage (e.g., seeds, seedlings, adults) to use in restoration. Should material be collected from the wild if possible, or taken from controlled growth conditions in greenhouses, gardens, and nurseries? What is the effect of the number of seeds, their genotype, and age on population establishment, and how do these characteristics interact with environmental factors among restoration sites? What are appropriate pre-planting treatments to the material or sites that could amplify establishment? How can natural seed and pollen dispersers be reestablished so that reproduction can be successful and gene flow among populations can be possible? Such questions bridge demographic and genetic considerations at the level of populations, communities, and landscapes (Guerrant 1996) and are being examined in deciduous forests in Massachusetts and long-leaf pine forests in South Carolina (Primack 1996).

Conclusions

We have emphasized that restorations provide a unique opportunity for testing fundamental predictions made from the theory of population genetics and ecology, while aiding the theory and practice of restoration. Restoration research includes a wide array of life forms exhibiting a range of life histories and interspecific interactions. Tests take place in the wild, typically on small populations in which both the demographic and genetic structure can be controlled. The opportunity exists to manipulate species interactions to observe the effects of mutualists, pests, and competitors on population establishment and growth, providing links between population and community ecology. The results of such research will contribute to improved restoration practice and success of restorations over the long term.

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