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TOWARD SUCCESSFUL REINTRODUCTIONS: THE COMBINED IMPORTANCE OF SPECIES TRAITS, SITE QUALITY, AND RESTORATION TECHNIQUE

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ABSTRACT

Reintroduction of endangered plant species may be necessary to protect them from extinction, provide connectivity between populations, and reach recovery goals under the U.S. Endangered Species Act. But what factors affect reintroduction success? And which matter more: traits inherent to the species, qualities of the site, or reintroduction technique? Here I propose that all three interact. First, reintroduction success will be highest for endangered species that share traits with non-rare native species, invasive plants, and species that excel in restoration plantings as reviewed from the ecological literature. Ten traits are identified as common to at least two of these groups. Second, reintroductions will do best in habitats ecologically similar to existing wild populations and with few local threats, such as non-native plants and herbivores. And third, the methods used to establish plants, such as planting seeds vs. transplants or selecting appropriate microsites, will influence outcomes. For any reintroduction project, potential pitfalls associated with a particular species, site, or technique may be overcome by integrating information from all three areas. Conducting reintroductions as designed experiments that test clearly stated hypotheses will maximize the amount and quality of information gained from each project and support adaptive management.

Key words: endangered species, extinction, plant trait, reintroduction, review.

INTRODUCTION

Endangered species reintroduction is necessary when too few populations exist in the wild to sustain long-term viability. It may be required to meet the objectives of Recovery Plans when their criteria call for additional populations in areas where a species has been extirpated. In addition, reintroduction may be implemented to mitigate for population losses caused by habitat development or changes in management priorities, but mitigation of this sort is much more controversial and fraught with ethical concerns (e.g., Allen 1994). In a review of 181 Recovery Plans for endangered species, one study (Hoekstra et al. 2002) found that 72% of plans call for some form of reintroduction. But reintroduction may be a costly process with no guarantee of success. Do some species lend themselves to reintroduction more easily than others?

Reintroduction is often regarded as a special form of habitat restoration that applies to rescuing or recovering endangered species (Maunder 1992; Falk et al. 1996; Armstrong and Seddon 2008). It faces many unique challenges due to the high value placed on the species targeted for improvement and the frequent knowledge gaps about individual species' needs (Guerrant and Kaye 2007). Reintroduction in general has been subject to such frequent failure that many regard it as unreliable (Fahselt 2007).

The reintroduction process has been outlined, evaluated, and updated over the last two decades by various workers around the world (e.g., Griffith et al. 1989; International Union for Conservation of Nature and Natural Resources [IUCN] 1995; Vallee et al. 2004; Kaye 2008; Menges 2008). Falk et al. (1996) provide a comprehensive overview of reintroduction. However, predicting which endangered species will perform best in a reintroduction has not been possible to date, partly because too few reintroductions have been published to draw broad generalizations.

Population reintroduction is a field still searching for a consistent vocabulary (Armstrong and Seddon 2008). Translocation is a term widely used for the same process, and can include the wholesale transplanting of individuals or populations from one wild site to another. Augmentation is the process of adding individuals to an existing population to increase its size and viability, and may be considered one form of reintroduction. Introduction is sometimes used as a synonym for reintroduction or translocation, but also describes the process of non-native and invasive species movement into a new region. I use the term reintroduction here inclusively to include all forms of placing plant materials into occupied or unoccupied sites of an endangered species within its historic range or ecoregion, with the assumption that a species may have occurred in any piece of appropriate habitat at some point in the

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past even if there is no supporting historic documentation.

Over 740 plant taxa are listed by the U.S. Fish and Wildlife Service as Threatened or Endangered *http://ecos.fws.gov/tess_public/SpeciesReport.do* (May 2009). With so many species needing support from conservationists, funding is unlikely to be available for a reintroduction program for all of them. Criteria for selecting species that are most likely to succeed in a reintroduction program are therefore urgently needed, and this will help maximize our efficiency. Also, species targeted for reintroduction that have a low chance of success will need additional effort, and this effort will be assisted if we are able to anticipate and plan for problems.

In this paper, I suggest that three primary factors interact to control reintroduction success (defined here as establishment, growth, and formation of a viable population, but see Pavlik [1996] for a comprehensive discussion of success in this context) and, when considered together, can improve reintroduction of rare species in general. These factors include plant traits inherent to the species, habitat conditions at the reintroduction site, and reintroduction technique. I consider each factor individually, then conclude with a discussion of how they interact.

PLANT TRAITS

Plant traits have been used to predict species response to disturbance (McIntyre et al. 1995), competitive ability (Grace 1990; Goldberg 1996), and invasiveness (Baker 1974; Sakai et al. 2001), for example. Since plant traits may have predictive power, an evaluation of rare species based on specific traits may help identify species most suitable for reintroduction. In order to develop a list of likely traits for this purpose, I consulted reviews of plant traits in three topic areas based on the hypotheses that reintroduction success will be highest for rare species that share traits with:

1. non-rare native species (or have traits opposite of typical rare species),
2. invasive plants, and
3. species that excel in restoration plantings.

These three areas were selected because traits inherent to rarity may make species more vulnerable to rapid extirpation at a new location, species that share traits with invasive species may tend to do well and spread when placed at a new site, and rare plants most like those that succeed in restorations may do best at the establishment and colonization phase. I looked for plant traits common to at least two of these categories to develop a preliminary list of plant traits that identify species that are "most likely to succeed."

A Synthesis of Reviews

Thorough reviews of the predictive power of plant traits in each of these topic areas are available (Table 1). For traits associated with rarity, I consulted three large reviews. Murray et al. (2002) searched for life history and ecological traits that consistently separate rare and common species. Their paper is really two papers in one; species in general from 54 comparative studies were examined from the global literature, and 700 eucalypt species in Australia were evaluated from their own data. Farnsworth and Ogurcak (2008) examined 71 rare plant species in New England to determine if species with shared traits showed similar fates of range shift and population extirpation. Hegde and Ellstrand (1999) looked at the well-studied floras of California and the British Isles to identify life history differences between species known to be rare or common.

Two reviews by Kolar and Lodge (2001) and Hayes and Barry (2008) were used to identify traits of invasive species. In the first, the authors reviewed 16 publications (half on plants) on invasions to identify traits of successful invaders. The second paper added 33 more studies to those reviewed in the first to identify independently verified predictors of invasion or establishment success of non-native species across multiple biological groups, including plants.

Traits of plants that grow well in ecological restorations were identified by Pywell et al. (2003). They performed a meta-analysis of 25 experiments with a cumulative total of 58 species to identify traits that predicted performance in field restorations in agricultural lowland Britain. Forbs (45 species) and grasses (13 species) were analyzed separately.

A total of 38 plant traits were identified in this process that were significant in at least one review (Table 1). All of these traits may be considered hypotheses for characteristics of plants likely to do well when reintroduced. Traits were placed into categories of life history, plant size and growth, pollination, seed biology, habitat, history, and characteristics of the native range. Some reviews

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Table 1. Plant traits of rare and endangered species, invasives, and top performers in restoration. Each column represents a review or synthesis of a large data set, or a subset of one. Only traits that were statistically significant in the original review are included. Traits in bold are common to at least two categories. The sign of the trait indicates the direction of effect. For example, rare species tend to have short flowering periods (-) but invasives tend to have long flowering periods (+). Traits with no sign for a review were not examined or were not significant in that review.

	Rare & endangered				Invasive		Restoration	
Citation	Murray et al. 2002		Farnsworth & Ogurcak 2008	Hegde & Ellstrand 1999	Kolar & Lodge 2001	Hayes & Barry 2008	Pywell et al. 2003	
Trait	General	Eucalyptus					Forbs	Grasses
Life history								
Length of flowering/seed production period	-	-			+	+		
Iteroparous				+				
Length of juvenile period					-	-		
Longevity						+		
Obligate symbioses			+					
Ruderality							+	+
Vegetative reproduction/clonal growth					+	+	+	
Plant size and growth								
Competitive ability (via rosettes, choking growth, or allelopathy)	+,-						+	
Height		-		-	+	+		
Leaf area	-	-				+		
Taller than wide						+		
Pollination								
Insect pollen vector (vs. wind or selfer)	+		+			+		
Not monoecious or gynoecious						+		
Polygynous (many pistils or styles) (compared to hermaphroditic, monocarpic, dioecious)						+		
Self-pollinating	-							
Seed biology								
Number of seeds	-				+			
Seed or fruit size					-	+,-	-	
Variability in seed crop					-			
Long distance dispersal mechanism			-		+			
% germination							+	
Germination number	-							
Dormancy	-							
Germination requirements fulfilled in many environments, discontinuous germination					+*			
Autumn germination							+	+

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Seed biology (cont.)									
	Seed bank							+	
	Seedling growth rate							+	
Habitat									
	Elevation				-				
	pH							-	
	Soil fertility							+	-
	Stress tolerance							-	-
	Upland vs. wetland			+					
History									
	History of invasion					+	+		
	Family or genus invasive					+			
	Taxonomic group					+	+		
Native range									
	Range area/variation in habitats occupied	-				+	+	+	
	Geographic origin					+			
	Match between habitat at source and destination						+		
	At or near range limit			+					

included additional traits that applied to other biological groups besides plants, and in some cases I combined multiple traits into a single trait for simplicity. Therefore, the traits in Table 1 reflect my interpretation, in some cases, of the traits identified by the various studies in an effort to reconcile differences in terminology while maintaining the authors' intent. A total of ten traits (listed in bold) were common to at least two categories. Overlap among groups provides support for individual traits as predictors of reintroduction success because the overlap suggests some generality across contexts.

Traits of Plants Likely to Succeed in a Reintroduction

Taken together, the traits common to more than one category provide a starting point for a hypothetical list of characteristics of species that may be most adapted for reintroduction (Table 2). For example, plants with a life-history that includes a long flowering and/or fruiting period as well as vegetative reproduction or clonal growth may be good candidates for reintroduction because they are unlike most critically endangered species and share characteristics with invasives and species that do well in restorations. Plants that are competitive, tall and have large leaf area may perform well in reintroductions for similar reasons.

Plants with insect pollen vectors (as opposed to wind or self pollination) were both more likely to be rare and invasive. This apparent contradiction makes it difficult to identify a specific pollination mechanism as a reintroduction trait. Even so, a bet-hedging strategy for a reintroduction candidate would be a mixed-mating system based on generalist insect or wind pollination with self-compatibility and autogamy as a failsafe mechanism. High seed production is associated with invasiveness but not rarity, while small seed size is generally (but not always) associated with invasive species and restoration. There is a general ecological trade off between seed size, number, and seedling recruitment such that seed size tends to decline as seed production increases, but species with larger seeds tend to establish and compete better than small-seeded species (Jakobsson and Eriksson 2000).

Table 2. Traits of species likely to succeed in reintroduction.

1.	Long flowering/fruiting period
2.	Vegetative growth
3.	Competitive
4.	Tall
5.	Large leaf area
6.	Generalist pollination, mixed mating system
7.	High seed production, intermediate seed size
8.	Long distance dispersal mechanism
9.	Large geographic range and/or multiple habitats
10.	History of reintroduction success or taxonomic relationship to species with a history of success
11.	Plastic phenology that shifts with climate

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Species with intermediate seed weight may optimize seed production and seedling performance (Jakobsson and Eriksson 2000). Therefore, species that produce seeds of intermediate size in large numbers may stand the best chance of success during reintroduction. Another seed biology trait associated with reintroduction potential may be strong dispersal, since rare species tend to have poor dispersal mechanisms while invasives tend to be capable of long-distance dispersal (Trakhtenbrot et al. 2005).

At least one analysis in each category found that geographic range size and/or variation in the types of habitats occupied by the species was an important factor in explaining species behavior. For example, rare species tend to occur over small geographic areas and occupy specialized habitats while invasives tend to have relatively large home ranges, and forbs that recruit well in restorations tend to be habitat generalists.

A history of invasion is a strong predictor of species invasiveness in new areas, as is taxonomic relationship to other invasives (Kolar and Lodge 2001; Hayes and Barry 2008). For most endangered species, no previous attempts at reintroduction have been performed, but this is likely to change with time as more reintroductions are attempted and the results published. I suggest that a history of reintroduction success or relationship (same genus or family) to species with a prior record of successful establishment will be a useful trait in identifying reintroduction projects with a high likelihood of success.

Climate change can affect native species in predictable ways. Species decline and loss near Concord, Massachusetts, in Thoreau's woods was driven by climate change and the ability of species to adapt to temperature shifts (Willis et al. 2008). Species that persisted over the last 150 years as the climate warmed were those that tracked seasonal temperature and shifted their flowering times in response to year-to-year variation and long term trends. Plants that did not alter their phenology in response to the changing climate were more likely to become less abundant or die out. This response was shared among closely related taxa. Species that are able alter their flowering time as climate changes may have an advantage in reintroduction projects because climate already has changed in many areas and continues to change. Although a plastic phenology that shifts with climate was not identified as a significant trait in any of the studies reviewed in Table 1, its importance is a recent discovery and has obvious relevance to plant conservation. For that reason it is included among the traits of plants most likely to succeed in reintroductions (Table 2).

CHARACTERISTICS OF THE REINTRODUCTION SITE

Characteristics of the reintroduction site may be just as important as traits of the plant to be reintroduced. Reintroduction success may be highest in habitats ecologically similar to existing wild populations. For example, fitness of transplanted *Lotus scoparius* (Nutt.) Ottley was positively correlated with environmental similarity between the source population and the transplant site (Montalvo and Ellstrand 2000). Similarly, survival of *Castilleja levisecta* Greenm., an endangered species of the Pacific Northwest, was highest at reintroduction sites most similar in vegetation to the seed source (Lawrence and Kaye 2009). In both cases, geographic distance between source and receptor site had little or no correlation with plant performance.

Non-native species may pose one of the most significant obstacles to reintroduction at any given location. Establishment and growth of *Abronia umbellata* subsp. *breviflora* (Standl.) Munz on Pacific Coast beaches was strongly negatively correlated with vegetative cover of *Ammophila arenaria* (L.) Link, a highly invasive grass (Kaye 2004). Weed competition adversely affected transplant survival and growth of two endangered Australian plants (Jusaitis 2005). Growth of planted *Castilleja levisecta* was negatively correlated with abundance of non-native plants across ten sites (Lawrence and Kaye 2009). Invasive species are clearly a threat to endangered plants, and without their control reintroductions are likely to have limited success in general.

Site productivity may also affect reintroduction success and interact with invasive species abundance. For example, high nutrient sites and areas that have received nutrient addition have lower diversity and increased dominance in wetlands (Bedford et al. 1999) and forests (Gilliam 2006). Invasive plants in California ecosystems are disproportionately more frequent in areas with high productivity, and the high frequency of rare and endangered species in these ecosystems makes them especially vulnerable to competition from invasives (Seabloom et al. 2006). Finally, nutrient addition into low productivity sites makes them more vulnerable to invasion by exotics (e.g., Lake and Leishman 2004). Selecting sites with low productivity, or reducing productivity artificially, may improve the odds of reintroduction success, especially for endangered species that are typically non-dominant in their wild populations.

Removal of threats in general may be crucial for reintroduction success. Sites that have processes in place that are associated with the cause of a species' endangerment or inhibit major life history steps may be poor choices. Invasive weeds and increases in nutrient availability are obvious examples, but alterations of disturbance regimes in general, such as fire suppression (e.g., Kaye et al. 2001; Quintana-Ascencio et al. 2003; Menges and Quintana-Ascencio 2004), may threaten rare species. Herbivores also can suppress seedling recruitment (Maschinski et al. 2004) and transplant survival (Jusaitis 2005; Lawrence and Kaye 2008, 2009) of reintroduced species. Sites that are not managed for conservation or are subject to development may be threatened with alteration or destruction (i.e., habitat loss) in the long term.

REINTRODUCTION TECHNIQUE

The methods used to establish plants at a site may affect project outcomes. Soil amendment and planting season can have strong effects on plant success. Adding fertilizer and planting in the fall resulted in only 3% and 18% survival of *Erigeron decumbens* Nutt. and *Horkelia congesta* Douglas ex Hook., respectively, after four years, while omitting fertilizer combined with spring planting yielded 48% and 84% survival (Kaye and Brandt 2005). Fertilizer increased plant size and fecundity in *Abronia umbellata* transplanted to beaches, but had no effect on survival (Kaye 2004). In addition, fencing plants to protect them from herbivory can increase transplant survival (Wendelberger et al. 2007; Thorpe 2008).

Microsites selected for transplants can have a significant effect on transplant success (Jusaitis 2005). For example, gaps created by sod cutting increased survival of *Scorzonera humilis* L. at nutrient-rich sites but decreased it at nutrient-poor sites (Reckinger et al. 2009). Seeds of *Centaurea corymbosa* Pourr. planted in selected cliff microsites established plants with higher survival than seeds that fell at random in a wild population (Colas et al. 2008). Soil moisture in particular may be important for the establishment of some species (Maschinski et al. 2004). For example, topographic position in a restored wetland affected transplant survival of four rare species (Kaye and Brandt 2005).

Propagule type and size have been explored in a variety of studies, and in general, larger plants have better performance during reintroduction. Plants established as sown seeds tend to have lower survival than transplants (Guerrant 1996; Bowles et al. 1998; Jusaitis et al. 2004; Kaye 2004; Guerrant and Kaye 2007; Reckinger et al. 2009), but if seeds are plentiful, low establishment may be acceptable if plug production costs are high (Kaye and Cramer 2003). Also, smaller transplants may perform poorly compared to larger transplants (Wendelberger et al. 2007). In some cases, however, plant size seems to matter little for growth or survival (Alley and Affolter 2004).

In general, attempting reintroductions with more than one technique may be an optimal approach. Implementing reintroductions as designed experiments can serve simultaneously as a way to compare techniques or test hypotheses and a bet-hedging strategy to maximize the likelihood that at least one method will have high success (Guerrant and Kaye 2007; Kaye 2008).

CONCLUSION

Improvement in the success rates of reintroductions is urgently needed to support conservation efforts for many rare species. Predicting success and anticipating challenges will make conservation more efficient. If species performance in reintroduction can be predicted then scarce funds and other resources can be allocated to those most likely to succeed. The plant traits identified here (Tables 1, 2) as potential markers of species that may be pre-adapted for reintroduction should serve as a hypothesis to be tested when larger data sets on the results of many reintroduction projects are available. And until then, they may be used to assist with ranking species for reintroduction. But even if the traits hypothesized here accurately predict success, ranking species and funding recovery work based on these characteristics may not always be desirable. In fact, including traits that are opposite those of most rare plants, as done here, will leave out many endangered species in need of aggressive conservation.

I suggest that the three areas discussed in this paper interact to determine the results of reintroductions (Fig. 1). The importance of plant characteristics will depend on site qualities and planting methods. For example, species with many positive traits for growth and survival may perform well even at poor sites and require the least amount of effort. But as the number of positive traits that a species possesses declines, site quality and technique will increase in importance. In

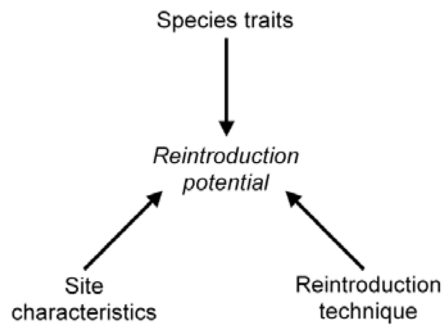

Fig. 1. Reintroduction potential of endangered species is affected by species traits, site characteristics, and reintroduction technique. Species without traits that improve their likelihood of reintroduction success may need better sites or more effort toward cultivation or planting methods.

cases where reintroduction will proceed despite a species' low predicted potential, managers may need to pick superior sites or prepare them better and/or put more effort into developing optimal planting practices.

Species conservation should emphasize protecting existing populations, but reintroduction is needed in some cases to stave off extinction and meet recovery goals.

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