MADROÑO, Vol. 53, No. 3, pp. 264–274, 2006

CONSERVATION OF PERIPHERAL PLANT POPULATIONS IN CALIFORNIA

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ABSTRACT

The conservation of peripheral plant populations is paradoxical. Populations occurring on the edge of a species' range tend to be smaller, more isolated, and more genetically and ecologically divergent than central populations. The combination of these characteristics can impart novel evolutionary potential and local ecological significance, thus heightening their conservation value, while also making them less viable and more prone to local extinction. Public policy supports the conservation of peripheral populations, despite the commonness of the species elsewhere. However, the conservation of significant peripheral populations of nonlisted plants has been arbitrary and ineffective. The absence of explicit criteria to determine the conservation value of peripheral plant populations, the lack of finer-scale data on plant distributions, and a general unawareness of their value have hindered efforts to conserve them. We review the conservation value of peripheral plant populations and, using California as an example, describe regulatory methods to improve their conservation. We also propose a scheme to assess a population's conservation value.

Key Words: California flora, CEQA, HCP, local rarity, NCCP, peripheral populations, rare plants.

Peripheral populations occur on the geographic edge of a species' range. Depending on the scale used to define them, peripheral populations can be completely isolated from conspecifics, and therefore considered disjunct, or can occur in closer proximity to other marginal populations. While the evolutionary significance of peripheral populations has long been recognized, other than for rare, threatened, or endangered species, their conservation value typically receives little attention.

In this paper, we review the conservation value of peripheral plant populations. Using California as an example, we highlight how regulatory policy can and should be utilized to conserve biologically and culturally significant peripheral populations of otherwise-common species. We also propose a scheme to assess the potential conservation value of peripheral populations.

Due to their geographically marginal location, peripheral populations tend to exhibit lower and more-variable densities and are more fragmented than central populations in a species' range (Fig. 1) (Mayr 1970; Lawton 1993; Channell and Lomolino 2000; Gaston 2003). For plants, peripheral populations are more likely to be influenced by different selective factors than central populations, including climate and soils, plant community assemblages, and disturbance regimes (e.g., fire intensity and interval). Ecologically distinct peripheral populations also can occur when geographically marginal populations occupy suboptimal or different habitats than more-central conspecifics (Soule 1973; Hoffmann and Blows 1994; Lesica and Allendorf 1995). Morphological or ecological divergence in peripheral populations resulting from differing geographic selection regimes is one form of clinal variation and can be a precursor to speciation (Mayr 1970; Garcia-Ramos and Kirkpatrick 1997). Due to the greater influence of population bottlenecks, founder effect, and genetic drift, peripheral populations can be genetically distinct from central populations. These differences in genetic structure can result in distinct genotypes and phenotypes and impart enhanced evolutionary potential for adaptation and speciation (Levin 1993; Garcia-Ramos and Kirkpatrick 1997; Lammi et al. 1999). Thus, the combination of geographic isolation and genetic divergence driven by directional selection can give peripheral populations novel evolutionary trajectories, in comparison to central populations (Lesica and Allendorf 1995; Nielsen et al. 2001; Gaston 2003). The isolation and decreased population size or abundance of peripheral populations, for instance, strongly favors the evolution of self-compatible breeding systems in otherwise self-incompatible species (Busch 2005).

Small, isolated populations, as often occur on the periphery of a species' range, also tend to have lower levels of heterozygosity and allelic variation than larger, more-central populations (Lesica and Allendorf 1992, 1995; Lawton 1993;

In comparison to core populations, peripheral populations tend to:

- be smaller,
- have more-variable densities,
- be ecologically distinctive,
- occur in marginal habitats,
- experience different selective regimes,
- have restricted gene flow,
- undergo greater rates of genetic drift,
- have less genetic variation,
- have increased population-level differentiation,
- have greater extirpation risk, and
- be morphologically similar

FIG. 1. Peripheral populations compared to core populations.

Lammi et al. 1999; Busch 2005) and thus may have decreased fitness and an increased risk of extirpation (Gaston 2003; Reed 2004). For this reason, the conservation of peripheral populations is controversial, because they tend to be less stable and are viewed by some as sink populations likely to be extirpated anyway, despite conservation efforts (Peterson 2001). By this rationale, the inclusion on state and federal endangered species lists of peripheral populations of species that are otherwise common and demonstrable secure elsewhere dilutes limited conservation resources that could be better focused on species with narrowly-restricted distributions or species of greater risk throughout their range (Peterson 2001).

However, the genetic diversity and structure and viability of a population is determined by many factors, including its degree of isolation and spatial pattern, gene flow, varying directional selection, and the species' reproductive strategies. Therefore, a population's viability can depend more on demographic structure and population dynamics (Bevill and Louda 1999) (e.g., whether the species is formerly common or historically rare [Brigham 2003]) than on its genetic structure. As well, lower levels of genetic diversity are not always associated with lower levels of fitness. For example, in a comparative study of central and peripheral populations of a rare European herb, *Lychnis viscaria* L. (Caryophyllaceae), Lammi et al. (1999) found that while genetic diversity was positively correlated with population size, no correlation was found between lower genetic diversity of peripheral populations and measured fitness characters such as seed set, seed germination, and seedling mass.

Contrary to Peterson (2001), under certain circumstances, geographic isolation actually predisposes peripheral populations to a greater survivorship than larger, more-central populations. In analyzing range contractions of 245 plant and animal species, Channell and Lomolino (2000) found that when species undergo catastrophic range contractions (>75%), populations on the edge of the range have significantly greater survivorship than core populations. This enhanced survivorship is the result of localized extinction events being primarily both anthropogenic and spatially autocorrelated. In other words, populations that persist the longest and act as refugia for a species tend to be those least (or last) affected by the spread of extinction forces (Channell and Lomolino 2000).

Thus, the conservation value of peripheral populations is paradoxical. On the one hand, peripheral populations can have enhanced ecological and evolutionary significance. On the other hand, this significance can be both a cause and a consequence of their isolation and small size and therefore correlated with reduced viability and increased extinction risk. While expert opinion is not unanimous about the conservation value of peripheral populations, the biological and intrinsic values of these populations are well documented and summarized as follows:

1) Their high potential for genetic distinctiveness and divergence can impart novel evolutionary pathways for future migration and speciation events (Levin 1993; Noss 1994; Lesica and Allendorf 1995; Garcia-Ramos and Kirkpatrick 1997; Nielsen et al. 2001; Gaston 2003).
2) The maintenance of genetic variation in the form of small, isolated populations contributes to long-term species survival and preservation of local genetic diversity (Millar and Libby 1991; Lesica and Allendorf 1992; Fiedler 1995; Lesica and Allendorf 1995; Lammi et al. 1999; Channell and Lomolino 2000; Caballos and Ehrlich 2002; Gapare and Aitken 2005; Gapare et al. 2005).
3) Even very widespread taxa (e.g., bison, sea otter, passenger pigeon, American elm, American chestnut) have been regionally extirpated or brought to the brink of extinction in a short time span (Nielsen et al. 2001).
4) Peripheral populations can have important local human values, (e.g., cultural, economic, and historical) regardless of how common the species may be elsewhere (Hunter and Hutchinson 1994; Gaston 2003).

Despite their conservation value, there are, at present, no explicit criteria to determine the conservation priority of peripheral populations. Lesica and Allendorf (1995) provide a useful theoretical framework for evaluating a population's conservation value that emphasizes the combination of geographic isolation and ecological distinctiveness as principal criteria. We agree that the degree of spatial isolation and ecological distinctiveness are the best criteria for assessing a population's conservation significance, especially in the absence of population genetics data. However, without some means to quantify or otherwise characterize spatial isolation or ecological distinctiveness, the conservation of these populations cannot be substantially improved during regional planning or the review of projects that may affect them. Furthermore, with the notable exception of Millar and Libby (1991), we find little guidance for conservation biologists on strategies to protect significant populations of widespread plants.

In this paper, we focus our discussion of conservation and land use planning strategies on California for the following reasons. First, California occupies a central biogeographic location and zone of ecological transition on the Pacific Coast of North America, so its floristic diversity includes many widespread taxa on the edge of their range. Second, California has the largest state flora in the nation and extraordinary topographic, geologic, and climatic habitat heterogeneity. Third, California has some of the strongest environmental regulations in the hemisphere, e.g., the California Environmental Quality Act (California Environmental Quality Act 2005) (CEQA), and the California Endangered Species Act; see Morey and Ikeda (2001) for an overview of state and federal laws and regulatory programs used to conserve California plants. Fourth, many of California's ecosystems and plant communities are highly threatened (Hobbs and Mooney 1998). California, for example, has a higher percentage of wetlands loss (an estimated 91 percent loss between the 1780's and 1980's) than any other state (Dahl 1990).

Reasons why Public Policy has been Arbitrary and Ineffective

Political Boundaries: a Conservation Tool and Impediment

Political boundaries, although not always arbitrary in their location, generally do not correspond with significant range boundaries for organisms. Interestingly, this lack of correspondence is less pronounced in the Old World, where political dynamics have more often coincided with constraints imposed by local terrain. In the New World, political boundaries were drawn after the onset of the Age of Reason and are more likely Cartesian or the results of formulistic procedures. As a result, political boundaries as a rule do not correspond with landscape discontinuities, with floristic provinces and districts, or with the conservation relevance of a population (Rodrigues and Gaston 2002).

Toward the periphery of many species' ranges, some populations are found to a lesser extent in the next political unit and are thus rare in that unit (Abbitt et al. 2000; Gaston 2003). A good example is *Sequoia sempervirens* (D. Don) Endl. (coast redwood) (Taxodiaceae), primarily a California species whose range extends into the state of Oregon, where it is rare. Other species exhibit the same pattern because the California Floristic Province extends into southwestern Oregon.

Because conservation efforts, both public and private, are primarily organized and managed within political units, conservation classification schemes routinely take differing geographic units into account in order to capture regional rarity as well as global rarity. Examples include the California Native Plant Society's (CNPS) Inventory of Rare and Endangered Plants, which includes List 2 (plants rare, threatened, or endangered in California, but more common elsewhere) and a RED code combination (i.e., rarity, endangerment, and distribution) that includes D = 1 (distribution is more or less widespread outside of California) (California Native Plant Society 2001). State heritage programs with ranks such as G5S1 (globally common and widespread, extremely rare and restricted in California) portray a similar geographic distribution (California Natural Diversity Database 2005). In these cases, the range of taxa extends into California to a sufficiently small degree that they are considered rare here.

Conservationists have typically accorded less concern to taxa in these circumstances than they have given to globally rare species. We agree with this general approach. Nevertheless, we contend that it is precisely those "state rare but globally widespread" species that provide the opportunity to reexamine peripheral populations for their conservation significance. Furthermore, a G5S1 RED code status illustrates an important consideration regarding the conservation of populations in these circumstances—namely, that they may warrant heightened conservation status, not because they happen to fall within a political boundary that makes them rare, but rather because they are much more likely to be peripheral populations having the attributes described earlier (Abbitt et al. 2000). Thus, conservationists seeking to preserve the unique and rare plants within their political boundaries also may be helping to conserve widespread species by focusing on their peripheral populations (see Hunter and Hutchinson 1994).

Conservation of Taxonomic Units Emphasizes Morphological Distinctiveness

Among the many important traits that allow plants to persist, morphological variation is crucial and is recognized for its importance. Coarse-level morphological variation is the preferred class of attributes used for plant identification and, before the advent of formal taxonomy, served as the basis for the so-called folk taxonomies. Moreover, morphological variation, in circumscribable and repeated patterns of distinctiveness, continues to be the primary basis for distinguishing among formal taxonomic units. In other words, variation among populations that results in morphological distinctness is more likely to lead to unique taxonomic status (Panchen 1992). Given that taxa (both species and subspecific taxa) are the principal units that are accorded conservation priority (when certain criteria are met), we argue that important classes of biologically significant variation are routinely overlooked as a basis for conservation efforts.

The significance of this issue is illustrated in the hypothetical examples shown in Figure 2. For these two scenarios, we consider the identical geographical distributions of populations: one large core range of populations in proximity to each other with an overall widespread geographic extent, and one small range of peripheral populations. In this case, the populations are also disjunct and largely isolated from the core. Under scenario A, disjunct populations are morphologically similar to the core populations, and thus given equal taxonomic status, called Taxon 1. In scenario B, while the populations also are closely related, the disjunct populations have distinctive morphological variation that leads to a unique taxonomic status, one for the core populations, Taxon 2, and one for the peripheral populations, Taxon 3. Thus, they are also sister species. These two scenarios portray the differing taxonomic results for two otherwise-equal geographic distributions of populations. What if the disjunct populations in scenario A (Taxon 1) have unique substrate or temperature tolerances? What if their underlying genomic variation is substantially different from the core population? What if they produce unique secondary compounds that afford them herbivore or disease resistance? All of these are possible and, indeed, are more likely in peripheral populations. Yet, they would not receive conservation status under scenario A, while they would under scenario B.

Assessing Conservation Criteria, Values, and Priorities

Although theoretical rationales for conserving peripheral populations are well developed, practical methods for evaluating their conservation value are compromised by the difficulty of collecting data, or by the fact that existing data are not organized specifically for this purpose. Nevertheless, a number of authors have proposed useful criteria for assessing the conservation value of peripheral or other special plant populations; these include isolation and distance, as well as genetic, environmental, evolutionary, life history, threat, and utilitarian attributes (Millar and Libby 1991; Holsinger 1992; Hunter and Hutchinson 1994; Schemske et al. 1994; Lesica and Allendorf 1995; Nielson et al. 2001).

Many of these categories overlap or are highly correlated. For example, environmentally distinctive populations are likely to be genetically distinctive, and thus may have greater evolutionary potential, depending on a number of other circumstances. Also, distantly isolated populations are more likely to be genetically distinctive, or occupy habitats that differ from core populations. As satisfying as these categories are biologically, they are not equal in terms of setting and implementing criteria for conservation.

Assessment of genetic distinctiveness should be a primary means for identifying peripheral populations of high conservation value. Indeed, because of the number of population genetic studies of plant populations, we have learned that significant levels of genetic variation often do not correlate with the features used for taxonomic demarcation. Genetic variation among populations is important because it is the basis for both environmental distinctiveness and evolutionary change. We agree that studies of these kinds should be conducted whenever possible. Unfortunately, genetic data are expensive and time consuming to retrieve and are not available for most California plant populations, with the exception perhaps of commercially important conifer species. Given the rate at which plant habitat is being lost and peripheral populations are disappearing, a practicable approach is needed to evaluate the conservation value of a given population.

Here, we propose three categories of criteria for evaluating the conservation significance of a peripheral population: 1) geographic isolation, 2) environmental distinctiveness, and 3) intrinsic human values. The first two criteria derive from Lesica and Allendorf (1995), who emphasize the importance of genetic drift and intensity of selection. The third criterion derives from many sources, but is well articulated by Hunter and Hutchinson (1994). These three attributes are the easiest to assess among all the criteria discussed above. Those populations that meet one or a combination of these criteria should be accorded a greater conservation value. Those that are also threatened or endangered should be given even greater value.

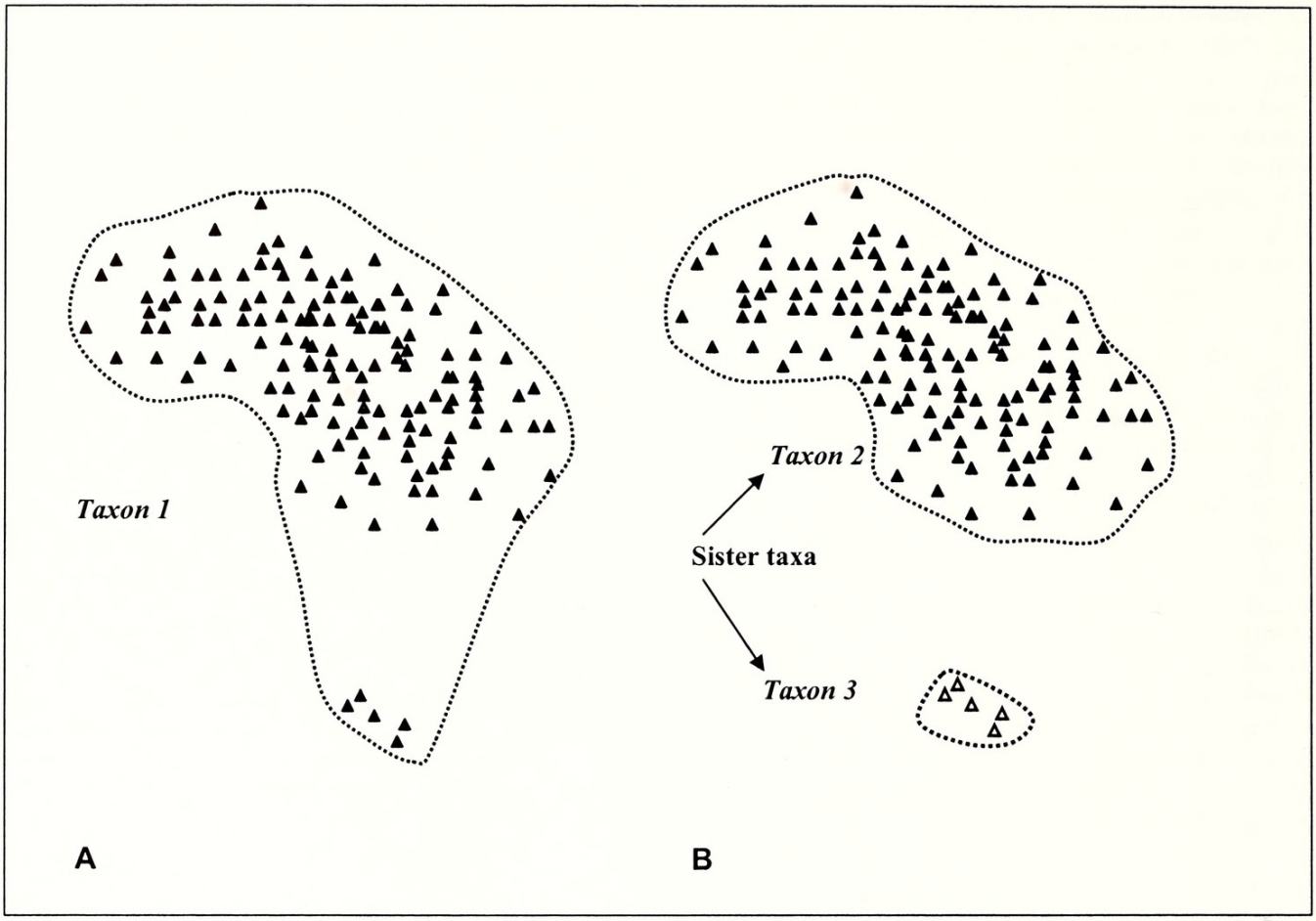

FIG. 2. Geographical distributions of two hypothetical scenarios that include a peripheral population. A) The peripheral populations are taxonomically part of *Taxon 1*. B) The peripheral populations, *Taxon 3*, are the sister species, or a closely related congener, to *Taxon 2*, the core population.

Geographic isolation criterion. Populations that are distant from core populations are, by definition, more likely to be on the periphery and thus be considered peripheral or, in some cases, disjunct populations. Also, the greater the distance from core populations, the more likely peripheral populations are to be genetically isolated and have distinctive traits with evolutionary importance. This criterion thus formalizes focusing on peripheral populations and has a significant biological rationale for inclusion.

This criterion should reflect distances that correspond to an evolutionarily significant degree of genetic isolation between peripheral and core populations. In some cases, nearest neighbor population distances will provide suitable comparative distances. However, consideration should be given to the overall geographic structure of the species' range and the specific methods used to characterize them (Gaston 2003; White 2004). The application of this criterion should also take into account life history attributes (e.g., mode of pollination, seed dispersal, life span). Because life histories vary greatly, no standard measure of geographic isolation can be utilized to assess the conservation significance of populations among diverse taxa.

Environmental distinctiveness criterion. Populations that occupy unusual or unique habitats are likely to have unique genetic traits, when compared to populations occupying core areas of the range (e.g., peripheral populations associated with community types, vegetation stands, or habitats that differ significantly from core populations). Populations in environmentally distinct locations are also more likely to have evolutionary significance. Thus, we consider environmental distinctiveness another critical category.

To more explicitly assess both environmental distinctiveness—and, to some degree, the functional spatial isolation of a peripheral population—we propose using the geographic subdivisions of Hickman (1993). Hickman utilizes a nested, four-tiered system of provinces, regions, subregions, and districts to divide California into meaningful biogeographic units. These subdivisions are, to the greatest extent possible, based on three main biologically relevant criteria: topography, climate, and vegetation type (Hickman 1993). For example, if a population is unique to a given subdivision or is isolated from conspecifics by one or more differing subdivisions, then this population would have, by definition, greater environmental and geographic distinctiveness

and isolation than would a peripheral population occurring in the same subdivision as the rest of its distribution. This approach benefits from being easily replicated outside of California by utilizing similar biogeographic subdivisions (e.g., those of Cronquist et al. 1972; Takhtajan 1986; Ricketts et al. 1999; Oregon Natural Heritage Program 2001).

Intrinsic human values criterion. Finally, conservation biology is highly value laden. The many, often idiosyncratic, and sometimes competing human values, ethics, and predilections play an important role in the conservation decision-making process (Noss 1994). There is general agreement that a population's cultural, economic, historic, and even aesthetic value enhances its conservation value. Local humans often assign important intrinsic values to local species, if for no other reason than they like having them on their landscape. Leopold (1949) captured this sentiment well: "Relegating grizzlies to Alaska is about like relegating happiness to heaven; one may never get there." Therefore, all things being equal, peripheral populations that have important human values would have greater conservation value than those that do not (see also Holsinger 1992). It is important to note that societal values change through time and that through education and effective public relations, the conservation community affects this change.

Examples of Populations that Merit Conservation

Here, we give three examples of taxa (Sitka spruce, lodgepole pine, and various orchid species) with relatively widespread California distributions possessing regionally significant populations with conservation value. Nomenclature follows Hickman (1993).

Picea sitchensis (Bong.) Carr. (Sitka spruce) (Pinaceae) is a Pacific Northwest coastal conifer and economically important timber tree, occurring from Alaska to northern California. Sitka spruce has a continuous distribution that terminates just south of Humboldt Bay in Humboldt County; however, a disjunct population occurs near Fort Bragg, Mendocino County, approximately 100 km to the south (Smith and Wheeler 1992; Lanner 1999).

In a comparative study of the genetic diversity of Sitka spruce throughout its range, Gapare et al. (2005) determined that peripheral and core populations have similar measures of heterozygosity; however, the only allele they classified as rare and localized was limited to disjunct and peripheral populations, including the Fort Bragg population. Gapare et al. (2005) demonstrate that peripheral and disjunct populations of this species have value for *in situ* conservation of rare alleles. In a related analysis, Gapare and Aitken (2005) found strong spatial genetic structure in peripheral populations, but not in core populations. This striking difference in the distribution of genetic variation among Sitka spruce population classes has important implications for size and location of *in situ* reserves and sampling strategies for *ex situ* conservation and research collections (Gapare and Aitken 2005).

Thus, this disjunct Fort Bragg Sitka spruce population has regional ecological, evolutionary, and economic significance because of its rare genetic geographic variation and dominance in local forest community structure.

Pinus contorta Dougl. ex Loud. (lodgepole pine) (Pinaceae) is a conifer widely distributed from the Yukon south to California and the Rocky Mountains, with a disjunct population in Baja California. It is extremely ecologically variable, with four named geographic subspecies (Critchfield 1957, 1980). It is a dominant tree species in many montane and coastal regions of western North America, and as such, is important both ecologically and economically. All four subspecies of lodgepole pine are represented in California, with northern California having much higher levels of heterozygosity and allelic diversity, compared to more northern and Rocky Mountain populations (Oliphant 1992).

In the Klamath Region of northern California, an undescribed lodgepole pine race, or ecotype, occurs on ultramafic substrates (serpentine soils). This race is referred to by Griffin and Critchfield (1972) as "an unnamed closed-cone race in the low mountains of Del Norte County" and by Critchfield (1980) as the "Del Norte race." Oliphant (1992) found that Del Norte race populations have low levels of expected heterozygosity and possess a suite of rare alleles; however, none are unique to the race. Kruckeberg (1967) demonstrated a differential growth response, with plants from non-ultramafic soils growing slower than plants from ultramafic soils when grown on an ultramafic substrate. Populations of the Del Norte race probably represent a distinct serpentine ecotype (Oliphant 1992). Though lodgepole pine is a common species in California and western North America, these Del Norte race populations occupy edaphically extreme sites and represent environmentally peripheral occurrences with unusual genotypes.

Coleman (1995) presents the county-wide and regional distribution and conservation implications of California's native orchid flora (Orchidaceae). Although many of California's orchid species are widely distributed, Coleman elucidates why marginal populations in southern California and the Santa Cruz Mountains are sufficiently isolated and threatened to warrant conservation efforts. These taxa all have geographic ranges that extend at least as far north as Washington.

According to Coleman (1995), orchid populations on the edge of their range in southern California are threatened for the following reasons: 1) populations are extremely rare in San Bernardino and San Diego Counties and large populations in San Luis Obispo and Santa Cruz Counties have been lost to urbanization (*Spiranthes romanzoffiana* Cham.); 2) recent attempts to locate southern California populations have been unsuccessful (*Spiranthes porrifolia* Lindley); 3) populations are so few and tiny that the species could be eliminated from an entire county by a single stochastic event or timber harvest (*Piperia leptopetala* Rydb.); and 4) species apparently have been extirpated from the Santa Cruz Mountains by habitat destruction (*Cypripedium fasciculatum* S. Watson and *C. montanum* Lindley).

Unlike the two previous examples, we have no data that indicates these orchid populations are genetically or environmentally distinct. Orchids are however one of the most charismatic components of the California flora and are revered by lay naturalists and biologists alike for their beauty and unusual reproductive biology. For example, southern and central California alone has over six orchid societies, and their importance in the horticultural trade is manifest. Therefore, we contend that given the intrinsic value placed upon these species, their regional rarity, and documented habitat loss and range contractions, these scarce southern California and Santa Cruz Mountains orchid populations warrant protection during regional conservation planning efforts and review of projects potentially impacting or eliminating them.

Regulatory Process

California Environmental Quality Act

Here we review certain regulatory programs that could be more effectively used to conserve significant peripheral plant populations. In doing so, we aim to better integrate current understandings about the biological attributes of peripheral and disjunct populations with the broader aims of the California regulatory framework.

CEQA, together with the California and federal Endangered Species Acts (CESA and FESA, respectively), is a principal tool used to conserve rare and endangered species in California. CEQA is landmark legislation that requires (with some exceptions) that potentially significant environmental impacts resulting from a proposed project (e.g., a housing development, dam installation, or timber harvesting plan) be disclosed to the public and reviewing state agencies. Furthermore, CEQA (section 21002) states that (again, with exceptions) public agencies should not approve projects that do not include feasible alternatives or mitigations that will avoid or substantially lessen significant effects, when such feasible alternatives or mitigations exist (California Environmental Quality Act 2005). Article 9 of CEQA, Contents of Environmental Impact Reports [section 15125 (c)], states "Knowledge of the regional setting is critical to the assessment of environmental impacts. Special emphasis should be placed on environmental resources that are rare or unique to that region and would be affected by the project."

CEQA is of fundamental importance to plant conservation, because it addresses potential impacts to any species that can be shown to meet the criteria for state or federal listing (section 15380[d]) (California Environmental Quality Act 2005), as well as to CESA and FESA listed species. Yet, to our knowledge, CEQA rarely has been utilized to protect peripheral or otherwise locally significant populations of widespread plant species if the species could not be considered endangered, rare, or threatened pursuant to CEQA (section 15380[d]). Despite this, a fair argument can be made by public agencies and conservationists that potentially significant impacts to these populations must be disclosed and avoided if: 1) the population is locally rare or unique (pursuant to CEQA section 15125 [c]) and therefore may have intraspecific variation and potential evolutionary significance; 2) the population has regionally significant ecological importance; and 3) the population has local cultural, economic, or historic value.

Regional Conservation Planning

In California, land use planning on nonfederal lands is done on the local scale—most commonly through municipal and county general plans. However, regional planning also occurs under the auspices of state Natural Community Conservation Plans (NCCPs) Natural Community Conservation Planning Act (2002) and federal Habitat Conservation Plans (HCPs). NCCPs and HCPs in California are regional conservation planning tools used to protect habitats of CESA and FESA listed and potentially listed species across a large area. A principal objective of NCCPs is to bring about species recovery by protecting natural communities on which the species depends. The principal federal objective of an HCP is to minimize and mitigate impacts to listed species to the maximum extent practicable. Land owners often enter into HCPs because it is the only means to receive an incidental take permit for a federally listed species. An incidental take permit is a permit to incidentally "take" (kill) a listed species during the course of an otherwise-legal activity.

NCCPs and HCPs both hold greater promise in conserving listed species and significant por-

tions of their habitat, or even entire ecosystems, than project-by-project mitigations (Noss et al. 1997; Rolfe 2001; Hopkins 2004). Regional conservation plans are also potentially much more effective in protecting habitats and species from large-scale, spatially autocorrelated threats such as urbanization, climate change, sea-level rise, and invasive species, most of which typically are not addressed or mitigated for effectively by smaller projects outside the HCP/NCCP realm. Regional conservation planning is potentially more effective in addressing cumulative impacts than are multiple, smaller-scale projects subjected to CEQA individually (Noss et al. 1997; Hopkins 2004). This is because cumulative impacts assessment is essentially a large-scale and rate-determined process not well suited to smaller, multiple, ongoing, regionally concentrated projects such as timber harvesting plans in a watershed or urban sprawl in the Central Valley.

However, as reviewed by Rolfe (2001), NCCPs and HCPs have significant shortcomings and incongruous objectives due to their reliance on take permits under FESA Section 10(a) and CESA Section 2835. Simply put, the FESA and CESA are reactive responses to species in jeopardy of extinction, while regional conservation plans are ostensibly a proactive approach to prevent the decline of species in the first place (Rolfe 2001). While NCCPs aim to promote multispecies and multihabitat management and the conservation of broad-based natural communities and species diversity, the impetus to initiate one is typically the conservation of listed or potentially listed species.

County general plans and ordinances are another important yet underutilized tool to conserve peripheral populations and other locally significant species and habitats. Santa Cruz County, for instance, has a "Sensitive Habitats Protection Ordinance" that requires that no development activities or land disturbance that results in disturbance to ". . . locally unique plants and animals or their habitats" can occur until a biotic review is conducted and necessary mitigation measures are developed to protect the habitat (Santa Cruz County Planning Department 2005). The Ventura County, California General Plan specifies that "locally important species/communities" are a significant biological resource to preserve and protect (Ventura County 1988).

Millar and Libby (1991) suggest that important populations of widespread species be conserved, in part, by the creation of "genetic resource management units" (GRMUs). These GRMUs can be, in essence, wilderness areas, botanical areas, or lands covered by a NCCP/HCP, if their management objective is the *in situ* conservation of biodiversity at the regional genetic-variation level. We agree with Millar and Libby (1991) on the necessity of creating GRMUs to conserve regional genetic diversity, and we recognize that simply by protecting large areas, NCCPs and HCPs can also protect significant peripheral populations. However, the full potential of regional conservation plans and other designated conservation areas in protecting regionally significant peripheral populations cannot be realized until their importance is better appreciated, actual populations are identified, and most importantly, their conservation priority is integrated into the management objectives of these regional plans.

Currently, there are 22 NCCPs being developed in California and nine that have been approved and permitted. All of these NCCPs are joined with an HCP and are typically 50-to 80-year agreements. Together, these 31 NCCPs cover over seven million acres (28,328 km^2), representing approximately seven percent of California. This is, therefore, a propitious time to emphasize the significance of peripheral populations during regional planning.

Need for more Accurate Delineation of Local Floras

Closer scrutiny of local floras and phytogeographic patterns is required to identify peripheral populations having significant conservation value. A principal impediment to the conservation of locally significant peripheral populations is the relative absence of finer-scale data on species distributions. Presently, the general geographic distribution of common species, such as those not tracked by CNPS, is understood only at the county-level scale, (for example Munz 1959, 1968), and therefore is of limited use in conservation planning because the spatial scale is too coarse.

Recently, however, CNPS chapters and others have begun compiling regional lists of peripheral, disjunct, or what has been termed "locally rare" taxa, in an effort to conserve them (Lake 2004; Magney 2004). Other regional and county floras (such as Thomas 1961; Hoover 1970; Smith and Wheeler 1992), although outdated, provide important data on peripheral populations (many now extirpated). Thomas (1961), for instance, lists 181 taxa with their southern geographic limits and 61 taxa with their northern limits in the Santa Cruz Mountains. We encourage the continued documentation and compilation of local floras and peripheral populations and otherwise regionally significant plant lists as a first step in understanding their conservation value and protecting them where appropriate.

Local floras are also important tools for identifying where concentrations of regionally and locally significant populations occur (i.e., biodiversity hotspots, potential reserve sites,

and finer-scale ecological boundaries) (Araujo 2002; Leppig 2004). Heckard and Hickman (1984), for example, demonstrate how a detailed local flora can highlight the conservation significance of a location due to its high concentration of peripheral plant populations. In the absence of more-spatially explicit data on plant species distributions, locally significant peripheral plant populations will continue to be unknowingly extirpated with no attempt to conserve them.

Lastly, the variation in size of county-level political units—both within California and among states—hampers effective comparative analyses and uniform application of conservation criteria. To ameliorate this problem, we advocate the use of methodologies based on 5 km × 5 km grids for characterizing plant distributions. Although some limitations and cautionary notes should be considered when using these methodologies (White 1999, 2004), they have been used effectively elsewhere (IUCN 2001; Pearman and Dines 2002) to accurately describe plant spatial patterns.

Summary Considerations

The evolutionary significance—and therefore conservation value—of peripheral populations is well documented, as is the greater threat of their extirpation. However, in our opinion, their value has yet to enter the zeitgeist of the conservation community. Peripheral populations have remained, at best, a marginal component of conservation planning since Millar and Libby (1991) first called attention to the conservation of significant populations of widespread species 15 years ago. In this paper, we emphasize populations rather than taxa, genetic diversity over taxonomic diversity, and evolutionary potential and processes over floristic maintenance. Thus, we have attempted to change how conservationists view rarity and commonness, and the scale and structure at which rarity typically is assessed. We hope to have also stimulated discussion and debate on this subject.

Our goal here is not to throw out the existing conservation structure, with its emphasis on listed, endangered, and narrowly endemic species, but rather to shift the conservation paradigm to include a different and typically overlooked suite of rare plants—those on the frontiers of their range. Endangered species and species rare throughout their range should, of course, be accorded high conservation priority. However, to optimize conservation planning and the long-term persistence of floristic diversity, conservationists also need to look beyond rare and endangered species and their habitats. Not all peripheral populations are worthy of conservation, but many clearly are. Identifying which populations warrant conservation efforts poses a continuing challenge. More genetic data, a better understanding of how metapopulation theory applies to these populations, and an even more-explicit approach than we present here for assessing conservation significance will clearly help.

We acknowledge that conservation resources are scarce, and will likely remain so. However, in our view, placing greater conservation emphasis on certain important peripheral populations will not necessarily take scarce resources away from species in perhaps greater need; rather, it will enhance current conservation efforts and large-scale regional planning.

Acknowledgments

This paper stemmed from discussions of the California Native Plant Society Locally Rare Working Group. We thank that group, the California Department of Fish and Game Botanical Working Group, and the members of the Biodiversity Research and Education Center at Humboldt State University for helpful conversations about these ideas and for providing many useful comments, information, and insight. John C. Hunter and two anonymous reviewers provided numerous suggestions and careful review that greatly improved this manuscript.

Literature Cited

Abbitt, R. J. F., J. M. Scott, and D. S. Wilcove. 2000. The geography of vulnerability: incorporating species geography and human development patterns into conservation planning. Biological Conservation 96:169–175.

Araujo, M. B. 2002. Biodiversity hotspots and zones of transition. Conservation Biology 16:1662–1663.

Bevill, R. L. and M. Louda. 1999. Comparisons of rare and common species in the study of plant rarity. Conservation Biology 13:493–498.

Brigham, C. A. 2003. Factors affecting the persistence of formerly common and historically rare plants. Pp. 59–97 *in* C. A. Brigham and M. W. Schwartz (eds.), Population viability in plants. Springer-Verlag, Berlin, Germany.

Busch, J. W. 2005. The evolution of self-compatibility in geographically peripheral populations of *Leavenworthia alabamica* (Brassicaceae). American Journal of Botany 92:1503–1512.

Caballos, G. and P. R. Ehrlich. 2002. Mammal population losses and the extinction crisis. Science 296:904–907.

California Environmental Quality Act. 2005. Public resources code 21000-21177 and the CEQA guidelines (California Code of Regulations, Title 14, Division 6, Chapter 3, Sections 15000–15387). Available at: http://ceres.ca.gov/ceqa/

California Native Plant Society. 2001. Inventory of rare and endangered plants of California, 6th ed. Rare Plant Scientific Advisory Committee, D.P. Tibor, convening editor. California Native Plant Society. Sacramento, CA.

California Natural Diversity Database. 2005. California Department of Fish and Game, Natural

Diversity Database. May 2005. Special vascular plants, bryophytes, and lichens list.

CHANNELL, R. AND M. V. LOMOLINO. 2000. Dynamic biogeography and conservation of endangered species. Nature 403:84–86.

COLEMAN, R. A. 1995. The wild orchids of California. Cornell University Press, Ithaca, NY.

CRITCHFIELD, W. B. 1957. Geographic variation in *Pinus contorta*. Maria Moors Cabot Foundation. Publication No. 3. Harvard University, Cambridge, MA.

———. 1980. Genetics of lodgepole pine. Research Paper WO-37, USDA Forest Service, Washington, D.C.

CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, AND J. L. REVEAL. 1972. Intermountain flora, Vol. 1. The New York Botanical Garden, Bronx, NY.

DAHL, T. E. 1990. Wetland losses in the United States, 1780s to 1980s. U.S. Fish and Wildlife Service, Washington, DC.

FIEDLER, P. L. 1995. Rarity in the California flora: new thoughts on old ideas. Madroño 42:127–141.

GAPARE, W. J. AND S. N. AITKEN. 2005. Strong spatial genetic structure in peripheral but not core populations of Sitka spruce [*Picea sitchensis* (Bong.) Carr.]. Molecular Ecology 14:2659–2667.

GAPARE, W. J., S. N. AITKEN, AND C. E. RITLAND. 2005. Genetic diversity of core and peripheral Sitka spruce [*Picea sitchensis* (Bong.) Carr.] populations: implications for conservation of widespread species. Biological Conservation 123:113–123.

GARCIA-RAMOS, G. AND M. KIRKPATRICK. 1997. Genetic models of adaptation and gene flow in peripheral populations. Evolution 51:21–28.

GASTON, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford, England.

GRIFFIN, J. G. AND W. B. CRITCHFIELD. 1972. The distribution of forest trees in California. Research Paper PSW-82, U.S.D.A. Forest Service, Berkeley, CA.

HECKARD, L. R. AND J. C. HICKMAN. 1984. The phytogeographic significance of Snow Mountain, North Coast Ranges, California. Madroño 31: 30–47.

HICKMAN, J. C. (ed.). 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley, CA.

HOBBS, R. J. AND H. A. MOONEY. 1998. Broadening the extinction debate: population deletions and additions in California and western Australia. Conservation Biology 12:271–283.

HOFFMANN, A. A. AND M. W. BLOWS. 1994. Species borders: ecological and evolutionary perspectives. Trends in Evolution and Ecology 9:223–227.

HOLSINGER, K. E. 1992. Setting priorities for regional plant conservation programs. Rhodora 94:243–257.

HOOVER, R. F. 1970. The vascular plants of San Luis Obispo County, California. University of California Press, Berkeley, CA.

HOPKINS, J. 2004. Regional conservation planning in California: a guide. Institute for Ecological Health, Davis, CA. Available at: http://www.cnps.org/programs/conservation/NCCP-HCPs.htm

HUNTER, M. L., JR. AND A. HUTCHINSON. 1994. The virtues and shortcomings of parochialism: conserving species that are locally rare, but globally common. Conservation Biology 8:1163–1165.

IUCN. 2001. IUCN Red List Categories and Criteria version 3.1. IUCN, Gland, Switzerland and Cambridge, England.

KRUCKEBERG, A. R. 1967. Ecotypic response to ultramafic soils by some plant species of northwestern United States. Brittonia 19:133–151.

LAKE, D. 2004. Rare, unusual and significant plants of Alameda and Contra Costa Counties (seventh edition). California Native Plant Society, East Bay Chapter, Berkeley, CA.

LAMMI, A. P., P. SIIKAMAKI, AND K. MUSTAJARVI. 1999. Genetic diversity, population size, and fitness in central and peripheral populations of a rare plant *Lychnis viscaria*. Conservation Biology 13: 1069–1078.

LANNER, R. M. 1999. Conifers of California. Cachuma Press, Los Olivos, CA.

LAWTON, J. H. 1993. Range, population abundance and conservation. Trends in Ecology and Evolution 8:409–413.

LEOPOLD, A. 1949. A Sand County almanac. Oxford University Press, New York, NY.

LEPPIG, G. 2004. Rare plants of northern California coastal peatlands: patterns in phytogeography and endemism. Pp. 43–49 *in* M. Brooks, S. Carothers, and T. LaBanca (eds.), Ecology and management of northern California rare plants, proceedings. California Native Plant Society Press, Sacramento, CA.

LESICA, P. AND F. W. ALLENDORF. 1992. Are small populations of plants worth preserving? Conservation Biology 6:135–139.

——— AND ———. 1995. When are peripheral populations valuable for conservation? Conservation Biology 9:753–760.

LEVIN, D. A. 1993. Local speciation in plants: the rule not the exception. Systematic Botany 18:197–208.

MAGNEY, D. L. 2004. Checklist of Ventura County rare plants. (updated 5 April 2005) California Native Plant Society, Channel Islands Chapter, Ojai, California. Available at: http://www.cnpsci.org/

MAYR, E. 1970. Populations, species, and evolution. Harvard University Press, Cambridge, MA.

MILLAR, C. I. AND W. J. LIBBY. 1991. Strategies for conserving clinal, ecotypic, and disjunct population diversity in widespread species. Pp. 149–170 *in* D. A. Falk and K. E. Holsinger (eds.), Genetics and conservation of rare plants. Oxford University Press, New York, NY.

MOREY, S. AND D. IKEDA. 2001. Conserving plants with laws and programs under the Department of Fish and Game. Pp. 12–16 *in* Rare Plant Scientific Advisory Committee, D. P. Tibor (convening ed.), Inventory of rare and endangered plants of California, 6th ed. California Native Plant Society Press, Sacramento, CA.

MUNZ, P. A. 1959. A California flora. In collaboration with D. D. Keck. University of California Press, Berkeley, CA.

———. 1968. Supplement to a California flora. University of California Press, Berkeley, CA.

NATURAL COMMUNITY CONSERVATION PLANNING ACT. 2002. California Fish and Game Code, 2005 edition, Sections 2800–2835.

NIELSEN, J. L., J. M. SCOTT, AND J. L. AYCRIGG. 2001. Endangered species and peripheral populations:

cause for conservation. Endangered Species Update 18:194–197.

NOSS, R. F. 1994. Some principles of conservation biology, as they apply to environmental law. Chicago-Kent Law Review 69:893–909.

———, M. A. O'CONNELL, AND D. D. MURPHY. 1997. The science of conservation planning: habitat conservation under the Endangered Species Act. Island Press, Washington, DC.

OLIPHANT, J. M. 1992. Geographic variation of lodgepole pine in northern California. M.S. thesis. Humboldt State University, Arcata, CA.

OREGON NATURAL HERITAGE PROGRAM. 2001. Rare, threatened, and endangered plants and animals of Oregon. Oregon Natural Heritage Program, Portland, OR.

PANCHEN, A. L. 1992. Classification, evolution, and the nature of biology. Cambridge University Press, Cambridge, England.

PEARMAN, C. D. and T. D. DINES (eds.). 2002. New atlas of the British and Irish flora. Oxford University Press, Oxford, England.

PETERSON, A. T. 2001. Endangered species and peripheral populations: cause for reflection. Endangered Species Update 18:30–31.

REED, H. R. 2004. Relationship between population size and fitness. Conservation Biology 19:563–568.

RICKETTS, T. H., E. DINERSTEIN, D. M. OLSON, C. J. LOUCKS, W. EICHBAUM, D. DELLASALA, K. KAVANAGH, P. HEDAO, P. T. HURLEY, K. M. CARNEY, R. ABELL, AND S. WALTERS. 1999. Terrestrial ecoregions of North America: a conservation assessment. Island Press, Washington, DC.

RODRIGUES, A. S. L. AND K. J. GASTON. 2002. Rarity and conservation planning across geopolitical units. Conservation Biology 16:674–682.

ROLFE, A. 2001. Understanding the political realities of regional conservation planning. Fremontia 29(3–4): 13–18.

SANTA CRUZ COUNTY PLANNING DEPARTMENT. 2005. The sensitive habitats protection ordinance. Santa Cruz County Code, Title 16, Chapter 16.32, Santa Cruz, CA. Available at: http://www.sccoplanning.com

SCHEMSKE, D. W., B. C. HUSBAND, M. H. RUCHELSHAUS, C. GOODWILLIE, I. M. PARKER, AND J. G. BISHOP. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584–606.

SMITH, G. L. AND C. R. WHEELER. 1992. A flora of the vascular plants of Mendocino County, California. University of San Francisco, San Francisco, CA.

SOULE, M. 1973. The epistatis cycle: a theory of marginal populations. Pp. 165–187 *in* R. F. Johnston, P. W. Frank, and C. D. Michener (eds.), Annual review of ecology and systematics, Vol. 4. Annual Reviews Inc., Palo Alto, CA.

TAKHTAJAN, A. 1986. Floristic regions of the world. University of California Press, Berkeley, CA.

THOMAS, J. H. 1961. Flora of the Santa Cruz Mountains of California. Stanford University Press, Stanford, CA.

VENTURA COUNTY. 1988. Ventura County general plan goals, policies, and programs. Amended 16 September 1997. Ventura County Board of Supervisors, Ventura, CA.

WHITE, J. W. 1999. Rarity and the phylogeography of the large-flowered *Piptolobi* of *Astragalus* (Fabaceae). Ph.D. dissertation, Michigan State University, East Lansing, MI.

———. 2004. Range size, error rates, and the geometry of rare species distributions. Pp. 11–22 *in* M. Brooks, S. Carothers, and T. LaBanca (eds.), Ecology and management of northern California rare plants, proceedings. California Native Plant Society Press, Sacramento, CA.