DOCKET
07-AFC-5
DATE JAN 04 2010
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California Native Plant Society
2707 K Street, Suite 1
Sacramento CA, 95816

STATE OF CALIFORNIA
State Energy Resources
Conservation and Development Commission

In the Matter of:	)	
The Application for Certification	)	DOCKET NO. 07-AFC-5
for the Ivanpah Solar Electric	)	
Generating System	)	

INTERVENOR CALIFORNIA NATIVE PLANT SOCIETY

Rebuttal Testimony of California Native Plant Society

Docket 07-AFC-5

January 4, 2010

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BIOLOGICAL RESOURCES

B. Exhibit List (* denotes new exhibits included with this submittal)

Doc. no.	Author and title
*1009	Sawyer, J., T. Keeler-Wolf, and J. Evens. 2009. A Manual of California Vegetation, 2nd Edition. California Native Plant Society Press: Sacramento, CA, pp. 566-569.
*1010	Hampe, A., and R. Petit. 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters 8: 461-467.
*1011	Lesica, P. and F. Allendorf. 1995. When are peripheral populations valuable for conservation? Conservation Biology 9(4): 753-760.

Special Status Plants and Intact Vegetation Communities

In response to the applicant's disagreements with conclusions reached in the FSA regarding impacts to special status plants, stated by the applicant in their opening testimony, final prehearing conference statement, and during issues workshops, the California Native Plant Society (CNPS) would like to emphasize the importance of plants occurring on the margins of their population ranges.

As noted in both the FSA and in CNPS opening testimony, peripheral populations are important for the long-term conservation of genetic diversity and evolutionary potential of a species, particularly within the context of uncertain climatic changes to their habitat (Hampe and Petit, 2005; Lesica and Allendorf, 1995).

CNPS would like to emphasize the contradictory approach to climate change mitigation represented by siting the project in its currently proposed location. One of the benefits of utility-scale solar projects will be their reduction of greenhouse gas emissions resulting from decreased need to rely on the combustion of fossil fuels for energy. However, if the implementation of this climate change mitigation strategy (greenhouse gas reduction) comes at the expense of reducing the native biodiversity of intact biotic communities (desert tortoise habitat, high quality vegetation alliances) then the benefit of the project is greatly reduced.

The Ivanpah Valley fan site is a large intact area of creosote-bursage scrub that is relatively free of weeds. The FSA describes the site as "particularly high quality in terms of species richness and diversity, including rich cactus and succulent diversity, creosote rings, micro-topographic diversity (upon which several of the special-status species depend), and currently contains relatively few non-native plants." (FSA, Biological Resources p. 6.2-37).

In A Manual of California Vegetation, (Sawyer et al., 2008) the authors describe threats to the Larrea tridentata-Ambrosia dumosa Shrubland Alliance (Creosote bush-white burr sage scrub) found at the proposed site as follows: "The presence of several non-native plants, particularly Brassica tournefortii, Bromus spp., and Schismus spp., has greatly increased fire frequencies and led to the degradation and destruction of many hectares of this alliance. Long-term, intensive grazing, OHV activity, mining, and military operations have also left their mark.... We need to identify, monitor, and manage areas free of these degrading influences" (page 568).

In addition, the authors state that Creosote bush-white burr sage scrub associations occurring with Pleuraphis rigida (Big galleta grass), and "those with a diverse shrub layer are G1/S1" (page 566). The G1/S1 (Global/ State) status rank means that the plant community is considered globally/state uncommon with "fewer than 6 viable occurences worldwide/statewide, and/or up to 518 hectares" (page 45). The Ivanpah site plant community has galleta grass and a diverse shrub layer. The qualities of this site, as well as similar areas throughout the Ivanpah Valley and indeed the California Desert Conservation Area are just those types of wild lands that our climate change strategies should be addressing through protection, rather than destruction.

**California Energy Resources Conservation
and Development Commission**

In the Matter of: APPLICATION FOR CERTIFICATION FOR THE IVANPAH SOLAR ELECTRIC GENERATING SYSTEM	DOCKET NO. 07-AFC-5

DECLARATION OF SERVICE

I, Greg Suba, declare that on January 4, 2010, I served and filed copies of the attached Rebuttal Testimony of Intervenor California Native Plant Society, dated January 4, 2010. The original document, filed with the Docket Unit, is accompanied by a copy of the most recent Proof of Service list, located on the web page for this project at: www.energy.ca.gov/sitingcases/ivanpah]. The document has been sent to the other parties in this proceeding (as shown on the Proof of Service list) and to the Commission's Docket Unit, in the following manner:

(Check all that Apply)
FOR SERVICE TO ALL OTHER PARTIES:

__X__ sent electronically to all email addresses on the Proof of Service list;
__X__ by personal delivery or by depositing in the United States mail at with first-class postage thereon fully prepaid and addressed as provided on the Proof of Service list above to those addresses NOT marked "email preferred."
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FOR FILING WITH THE ENERGY COMMISSION:
__X__ sending an original paper copy and one electronic copy, mailed and emailed respectively, to the address below (preferred method);
OR
_____ depositing in the mail an original and 12 paper copies, as follows:

CALIFORNIA ENERGY COMMISSION
Attn: Docket No.
1516 Ninth Street, MS-4
Sacramento, CA 95814-5512
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I declare under penalty of perjury that the foregoing is true and correct.

Greg Suba
Greg Suba

Sent via email to: sdeyoung@brightsourceenergy.com; tstewart@brightsourceenergy.com; jcarrier@ch2m.com; jdh@eslawfirm.com; e-recipient@caiso.com; tom_hurshman@blm.gov; Raymond_Lee@ca.blm.gov; dfgpalm@adelphia.net; tgulesserian@adamsbroadwell.com; mjconnor@westernwatersheds.org; gloria.smith@sierraclub.org; devorah.ancel@sierraclub.org; joanne.spalding@sierraclub.org; gssilliman@csupomona.edu; jbasofin@defenders.org; atomictoadranch@netzero.net; gsuba@cnps.org; thansen@cnps.org; granites@telis.org; bbrizzee@cc.sbcounty.gov; jbyron@energy.state.ca.us; jboyd@energy.state.ca.us; pkramer@energy.state.ca.us; jkessler@energy.state.ca.us; dratliff@energy.state.ca.us; publicadviser@energy.state.ca.us; docket@energy.state.ca.us; lbelenky@biologicaldiversity.org; ianderson@biologicaldiversity.org

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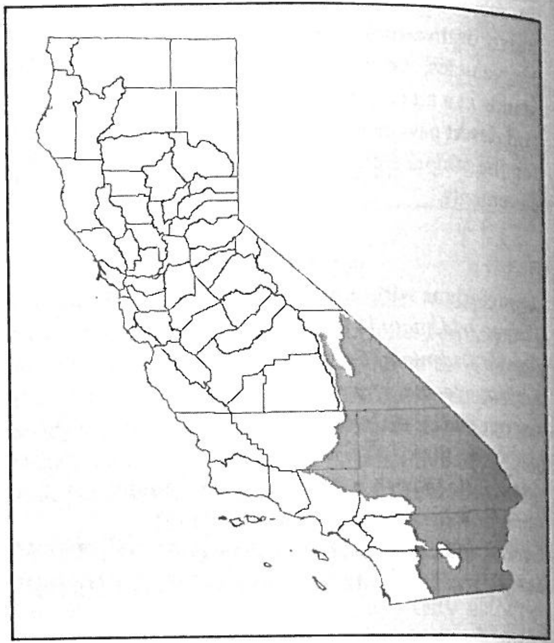
EXHIBIT 1009

Larrea tridentata–Ambrosia dumosa Shrubland Alliance

Creosote bush–white burr sage scrub

***Larrea tridentata* and *Ambrosia dumosa* are co-dominant in the shrub canopy** with *Ambrosia salsola, Amphipappus fremontii, Atriplex confertifolia, A. hymenelytra, A. polycarpa, Bebbia juncea, Croton californicus, Cylindropuntia acanthocarpa, C. ramosissima, Dalea mollissima, Echinocactus polycephalus, Encelia farinosa, E. virginensis, Ephedra* spp., *Eriogonum fasciculatum, Krameria* spp., *Lepidium fremontii, Lycium andersonii, Psorothamnus* spp., *Salazaria mexicana, Senna armata, Viguieria parishii,* and *Yucca schidigera*. Emergent *Fouquieria splendens* or *Yucca brevifolia* plants may be present at low cover. Shrubs < 3 m; canopy is open to intermittent, and may be two tiered. Herbaceous layer is open to intermittent with seasonal annuals.



Habitats: Minor washes and rills, alluvial fans, bajadas, upland slopes. Soils are well-drained, alluvial, colluvial, sandy, and sometimes underlain by a hardpan that may be calcareous and/or covered with desert pavement. **Elevation:** –75 m–1200 m.

Life History Traits of Principal Species

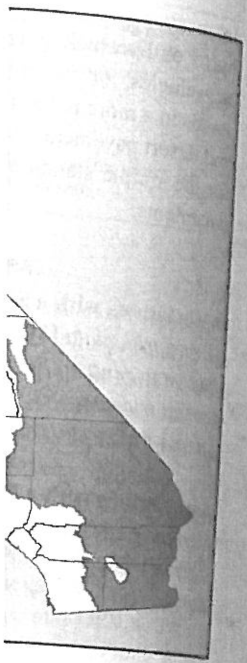
	Larrea tridentata	*Ambrosia dumosa*
Life forms	Shrub; drought deciduous	Shrub; drought deciduous; clonal
Seed storage	Soil	Soil
Seed longevity	Medium	Medium
Mode of dispersal	Animal; gravity; wind	Animal; tumbling
Germination agents	Chemical; heat	None
Mode of sprouting	Underground structures	Underground structure (root crowns)
Survivability after fire/disturbance	Fire-sensitive; no/low sprouter	Fire-sensitive; no/low sprouter (weak sprouter)
Disturbance-stimulated flowering	No	No
Reproductive range	Long-lived (maybe 100s to 1000s of years)	5–50 years
Recruitment	Low to high (secondary colonizer, depends on fire intensity)	High (on open ground)
Regional variation	Low	Low

Rarity ranking: G5 S5 (associations with *Pleuraphis ridiga* and those with a diverse shrub layer are G1 S1). **MCV:** Creosote bush–white bursage series. **NVCS:** *Larrea tridentata–Ambrosia dumosa* shrubland alliance. **Calveg:** Creosote bush. **Holland:** Mojave creosote bush scrub, Sonoran creosote bush scrub. **Munz:** Creosote bush scrub. **WHR:** Desert scrub.

Membership Rules

Both *Larrea tridentata* and *Ambrosia dumosa* ≥ 1% absolute cover in the shrub canopy; both species exceeding 2 × the cover of other shrub species (Keeler-Wolf et al. 1998b).

Both *L. tridentata* and *A. dumosa* ≥ 1% absolute cover in the shrub canopy; *A. dumosa* may be higher cover than *L. tridentata*. No shrub with cover greater than *L. tridentata* or *A. dumosa* with the following exceptions: *Acampthopappus sphaerocephalus, Bebbia juncea, Cylindropuntia acanthocarpa, Ephedra nevadensis, Ericameria teretefolia,* or *Krameria* spp.



covered with desert
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:ions with *Pleuraphis*
rub layer are G1 S1).
'sage series. **NVCS:**
dumosa shrubland
ı. **Holland:** Mojave
reosote bush scrub.
R: Desert scrub.

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ıopy; both species
'ub species (Keeler-

ɔsa ≥ 1% absolute
osa may be higher
with cover greater
vith the following
'ocephalus, Bebbia
ıcarpa, Ephedra
or *Krameria* spp.

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may have higher cover, but no more than 3 times (Thomas et al. 2004).

Remarks

Larrea tridentata is a very long-lived shrub, 10,000+ years as a clone, with low seedling recruitment (Vasek and Barbour 1977). It is an evergreen and extremely resistant to high temperatures and low precipitation. *L. tridentata* minimizes evapotranspiration by stomatal and water potential regulation daily and annually (Hamerlynck et al. 2002, Oechel et al. 1972, Ogle and Reynolds 2002). Its resinous leaves diminish transpiration more than assimilation (Meinzer et al. 1990). Further, the stem and foliage architecture minimizes self-shading under favorable photosynthetic conditions, whereas the leaves fold up and alter their angle to minimize direct solar radiation under periods of moisture stress (Ezcurra et al. 1992). Plants may die during severe droughts, though they typically persist longer than other shrubs and can sprout from the base when moisture returns.

Ambrosia dumosa is a short-lived shrub with relatively shallow roots. It dominates sandy substrates, rocky hills, or alluvial fans, and particularly older soils with caliche or clay layers. It tends to replace *L. tridentata* on soils with high clay content (McAuliffe 1988). Plants decline under long term, moderate-to-intense grazing (Marshall 1994), but they quickly colonize recently denuded sites (Vasek 1980).

Stands with taller *L. tridentata* and shorter *A. dumosa* shrubs represent the major vegetation type of California's hot deserts. This alliance covers approximately 67% of the central Mojave Desert (Thomas et al. 2004) and about 70% of the Colorado and Sonoran deserts in the state. It is the modal vegetation type of the bajadas, alluvial fans, and lower slopes. Conditions range from extremely hot dry sites with very low species diversity below sea level in Salton Sink to relatively diverse mesic sites and higher diversity at > 1100 m in the eastern Mojave Desert.

Closely related ecologically to this and other upland alliances of the hot deserts, the *Larrea tridentata* alliance is often a degraded version of this alliance; the *Ambrosia dumosa* and *Ambrosia salsola* alliances are a result of soil, grazing, or higher flood frequencies; the *Atriplex confertifolia, Coleogyne ramosissima, Grayia spinosa, Yucca schidigera,* and *Yucca brevifolia* alliances occur in moister, cooler settings; the *Atriplex hymenelytra* and *Larrea–Encelia farinosa* alliances exist in hotter, more exposed settings; and the *Atriplex polycarpa* and *Atriplex spinescens* alliances occupy heavy or alkaline soils.

Natural processes in the alliance include the effects of shifting moisture availability. Both *A. dumosa* and *L. tridentata* die following severe droughts, but *L. tridentata* typically persists longer and can sprout when moisture returns. *A. dumosa* establishes more readily from seed banks and off-site sources. A study of cleared sites in the eastern Mojave Desert (Vasek 1980) found rapid colonization by *A. dumosa, Cylindropuntia bigelovii, Encelia farinosa,* and *Stephanomeria pauciflora; L. tridentata* colonized only slowly.

Fire Characteristics

Both *Ambrosia dumosa* and *Larrea tridentata* exhibit limited sprouting ability after fire, and *L. tridentata* has resinous foliage that is highly flammable (Vasek 1979, 1983, Marshall 1995b). Low-intensity fires can cause up to 100% mortality in both *L. tridentata* and *A. dumosa,* but some shrubs can survive if crowns are only partially consumed. Mortality rates are probably related to rainfall conditions during the immediate postfire years, and both species may colonize successfully by seed from offsite sources in high rainfall years following a fire (Brooks and Minnich 2006). However, *A. dumosa* can colonize more rapidly after fire and may dominate alone for a number of years before both *L. tridentata* and *A. dumosa* regain similar pre-fire dominance.

Fire Characteristics

Fire-return interval	Truncated long
Seasonality	Spring–summer–fall
Size/extent	Small to moderate
Complexity	Low
Intensity	High
Severity	Moderate
Type	Passive-active crown fire
Regional knowledge	Hot deserts

Regional Status

Colorado Desert (322Ca–b, Cd). Stands are common in the western subsections, and are related at upper elevations to stands of the *Agave deserti, Viguiera parishii,* and *Larrea tridentata–Encelia farinosa* alliances. Lower elevation stands border *Atriplex polycarpa, Encelia farinosa, Fouquieria splendens,* and *Cylindropuntia bigelovii* alliances in Anza-Borrego Desert State Park (Keeler-Wolf et al. 1998b).

Mojave Desert (322A). Associations in this section contain from two to more than 20 shrub species in mid-desert settings. The many associations in the alliance sort into those of higher elevations, rocky slopes, bajadas, washes, and sandy substrates and basins. In Death Valley, the alliance exists adjacent to stands of the *Grayia spinosa, Atriplex confertifolia,* and other Great Basin alliances; in the southern subsections, stands are adjacent to those of the *Cylindropuntia bigelovii, Encelia farinosa,* and *Viguiera parishii* alliances (Annable 1985, Peterson 1984a, 1984b, Thomas et al. 2004).

Sonoran Desert (322B). Stands are simpler than in the Mojave Desert, likely because of low climatic and topographic variation in this section. Low density and low diversity stands occupy old dissected alluvial fans with desert pavement. A fine-grained matrix exists between stands of this alliance and those of the *Cylindropuntia bigelovii, Encelia farinosa,* and *Parkinsonia florida–Olneya tesota* alliances (Evens and Hartman 2007).

Southeastern Great Basin (341Fb–e). Stands exist in the Eureka and Saline valleys and in areas bordering the Mojave Desert. Stands merge with those of the *Atriplex confertifolia, Atriplex hymenelytra, Ephedra funerea,* and *Artemisia nova* alliances, with the latter two particularly on calcareous substrates. Northernmost stands in Eureka Valley are relatively simple with the *Larrea tridentata–Ambrosia dumosa–Psorothamnus fremontii* association (Thomas et al. 2004).

Southern California Mountains and Valleys (M262Bi). Stands occur in some of the lower reaches of the Little San Bernardino Mountains in Joshua Tree National Park (Keeler-Wolf et al. 2005).

Management Considerations

The presence of several non-native plants, particularly *Brassica tournefortii, Bromus* spp., and *Schismus* spp., has greatly increased fire frequencies and led to the degradation and destruction of many hectares of this alliance. Long-term, intensive grazing, OHV activity, mining, and military operations have also left their mark (Brooks 1999). We need to identify, monitor, and manage areas free of these degrading influences.

Associations

Bajada Associations

Larrea tridentata–Ambrosia dumosa [1], [2], [4], [5], [6]
Larrea tridentata–Ambrosia dumosa/cryptogamic crust [2]
Larrea tridentata–Ambrosia dumosa–Cylindropuntia ramosissima [5]
Larrea tridentata–Ambrosia dumosa–Encelia farinosa [4], [5]
Larrea tridentata–Ambrosia dumosa–Krameria erecta [5]
Larrea tridentata–Ambrosia dumosa–Krameria grayi [4], [5]
Larrea tridentata–Ambrosia dumosa–Lepidium fremontii [5]
Larrea tridentata–Ambrosia dumosa–Lycium andersonii [5]
Larrea tridentata–Ambrosia dumosa–Opuntia basilaris [5]
Larrea tridentata–Ambrosia dumosa–Psorothamnus arborescens [5]
Larrea tridentata–Ambrosia dumosa–Psorothamnus fremontii [5]
Larrea tridentata–Ambrosia dumosa–Psorothamnus schottii [3], [4]
Larrea tridentata–Ambrosia dumosa/Eriogonum inflatum [5]

Rocky, Upland Associations

Larrea tridentata–Ambrosia dumosa–Atriplex hymenelytra [3]
Larrea tridentata–Ambrosia dumosa–Amphipappus fremontii [5]

Larrea tridentata–Am
polyceph
Larrea tridentata–Am
funerea [
Larrea tridentata–Am
splendens
Larrea tridentata–Am
parishii [
Larrea tridentata–Am
angustifol

Higher-Elevation Ass

Larrea tridentata–Am
confertifol
Larrea tridentata–Amb
confertifol
arborescen
Larrea tridentata–Amb
acanthoca
Larrea tridentata–Amb
nevadensis
Larrea tridentata–Amb
viridis [5]
Larrea tridentata–Amb
cooperi [5]
Larrea tridentata–Amb
fasciculatu
Larrea tridentata–Amb
[5]
Larrea tridentata–Amb
sarothrae [5
Larrea tridentata–Amb
mexicana [5
Larrea tridentata–Ambro
schidigera [2

Wash Associations

Larrea tridentata–Ambro
salsola–Peta

Larrea tridentata–Ambrosia dumosa–Echinocactus polycephalus [5]

Larrea tridentata–Ambrosia dumosa–Ephedra funerea [5]

Larrea tridentata–Ambrosia dumosa–Fouquieria splendens [2]

Larrea tridentata–Ambrosia dumosa–Viguieria parishii [5]

Larrea tridentata–Ambrosia dumosa/Galium angustifolium–Lyrocarpa coulteri [3]

Higher-Elevation Associations

Larrea tridentata–Ambrosia dumosa–Atriplex confertifolia [1], [5]

Larrea tridentata–Ambrosia dumosa–Atriplex confertifolia–Psorothamnus arborescens [5], [6]

Larrea tridentata–Ambrosia dumosa–Cylindropuntia acanthocarpa [5]

Larrea tridentata–Ambrosia dumosa–Ephedra nevadensis [5]

Larrea tridentata–Ambrosia dumosa–Ephedra viridis [5]

Larrea tridentata–Ambrosia dumosa–Ericameria cooperi [5]

Larrea tridentata–Ambrosia dumosa–Eriogonum fasciculatum [5]

Larrea tridentata–Ambrosia dumosa–Grayia spinosa [5]

Larrea tridentata–Ambrosia dumosa–Gutierrezia sarothrae [5]

Larrea tridentata–Ambrosia dumosa–Salazaria mexicana [5]

Larrea tridentata–Ambrosia dumosa–Yucca schidigera [2], [4]

Wash Associations

Larrea tridentata–Ambrosia dumosa–Ambrosia salsola–Petalonyx thurberi [5]

Larrea tridentata–Ambrosia dumosa–Bebbia juncea [5]

Larrea tridentata–Ambrosia dumosa–Encelia virginensis [5]

Larrea tridentata–Ambrosia dumosa–Ephedra californica [5]

Larrea tridentata–Ambrosia dumosa–Olneya tesota [2]

Larrea tridentata–Ambrosia dumosa–Psorothamnus emoryi sandy [2], [3]

Larrea tridentata–Ambrosia dumosa–Psorothamnus spinosus [2]

Larrea tridentata–Ambrosia dumosa–Senna armata [2], [4]

Sandy or Basin Associations

Larrea tridentata–Ambrosia dumosa–Atriplex canescens [5]

Larrea tridentata–Ambrosia dumosa–Atriplex polycarpa [5]

Larrea tridentata–Ambrosia dumosa–Psorothamnus emoryi sandy [2], [3]

Larrea tridentata–Ambrosia dumosa/Dalea mollissima [5]

Larrea tridentata–Ambrosia dumosa/Pleuraphis rigida [2], [4], [5]

References

[1] Annable 1985, Brooks and Minnich 2006, Burk 1977, [2] Evens and Hartman 2007, Holzman 1994, Hunt 1966, Keeler-Wolf 2007b, [3] Keeler-Wolf et al. 1998b, [4] Keeler-Wolf et al. 2005, [5] Keeler-Wolf and Thomas 2000, MacMahon 1988, Marshall 1994, 1995b, McAuliffe 1988, [6] Peterson 1984a, 1984b, Reid et al. 1999, Sawyer and Keeler-Wolf 1995, Thomas et al. 2004, Thorne 1982, Turner 1982b, Turner and Brown 1982, Vasek and Barbour 1977.

EXHIBIT 1010

Ecology Letters, (2005) **8**: 461–467 doi: 10.1111/j.1461-0248.2005.00739.x

IDEAS AND PERSPECTIVES

Conserving biodiversity under climate change: the rear edge matters

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Abstract

Modern climate change is producing poleward range shifts of numerous taxa, communities and ecosystems worldwide. The response of species to changing environments is likely to be determined largely by population responses at range margins. In contrast to the expanding edge, the low-latitude limit (rear edge) of species ranges remains understudied, and the critical importance of rear edge populations as long-term stores of species' genetic diversity and foci of speciation has been little acknowledged. We review recent findings from the fossil record, phylogeography and ecology to illustrate that rear edge populations are often disproportionately important for the survival and evolution of biota. Their ecological features, dynamics and conservation requirements differ from those of populations in other parts of the range, and some commonly recommended conservation practices might therefore be of little use or even counterproductive for rear edge populations.

Keywords

Demography, diversification, extinction, genetic differentiation, glacial refugia, global change, leading edge, peripheral populations, Quaternary, trailing edge.

Ecology Letters (2005) 8: 461–467

INTRODUCTION: MARGINAL POPULATIONS, THE LEADING AND THE REAR EDGE

There is now ample evidence that modern climate change is reshuffling the geographic distributions of plant and animal species world-wide (Parmesan & Yohe 2003). The dynamics of those populations that inhabit the latitudinal margins of the distribution range are likely to be critically important in determining species' responses to expected climate change (e.g. Thomas *et al.* 2001; Iverson *et al.* 2004; Travis & Dytham 2004). Here, we argue that rear edge populations, defined as those populations residing at the current low-latitude margins of species' distribution ranges, are disproportionately important for the long-term conservation of genetic diversity, phylogenetic history and evolutionary potential of species and that their investigation and conservation deserve high priority.

Comparing the behaviour of local populations across species' distribution ranges has a long tradition (Brown *et al.* 1996). A major paradigm of this research is the 'centre-periphery hypothesis', which predicts that marginal populations are more prone to extinction and genetically less diverse than those from the centre, because they tend to occur in less favourable habitats and at lower and more variable densities (Lawton 1993; Vucetich & Waite 2003). Although the utility of this paradigm at local to regional scales is generally accepted, recent empirical work has challenged its significance at broad geographical scales (Channell & Lomolino 1999; Sagarin & Gaines 2002a,b; Vucetich & Waite 2003). In particular, phylogeographic surveys show that rangewide patterns of population genetic diversity are usually shaped by past climate-driven range dynamics (Hewitt 2000, 2004) rather than by demo-genetic stochasticity *per se*, as proposed in the centre-periphery model. As a consequence, marginal rather than central populations commonly harbour the bulk of species' genetic diversity (e.g. Petit *et al.* 2003; Hewitt 2004). In summary, the utility of the deterministic centre-periphery-model is limited in the context of range modifications driven by climatic changes.

During the past decade, a more dynamic view of present-day distribution ranges has increasingly been adopted in phylogeography, invasion biology and global change biology, and the demographic and evolutionary processes that accompany species expansions have attracted much attention (e.g. Sakai *et al.* 2001; Thomas *et al.* 2001; Petit *et al.* 2004). In particular, the 'leading edge' model of colonization, which states that range expansions involve mostly populations from the colonization front and are largely controlled by rare long-distance dispersal events followed by exponential population growth, has become a central paradigm in phylogeography, as it helps to explain the commonly observed poleward decrease of genetic diversity both within and among populations (Hewitt 1993, 2000).

In contrast, no theoretical study has investigated the behaviour of populations located at eroding range margins following climate change (see below), and there are only a handful of empirical studies addressing this issue. In principle, the behaviour at such distribution edge could range between two extremes: populations could become completely extirpated, resulting in latitudinal displacement of a species' range, or a varying fraction could persist, resulting in a simple expansion of the range into newly favourable regions without concomitant decline at the other extremity. We suggest reserving the term 'trailing edge' for the first situation; populations that inhabit trailing edges should therefore be at most slightly older than other populations of the range. A good example of this situation is provided by some boreal species such as spruce in North America, whose range has entirely shifted since the last ice age (Williams *et al.* 2004). In contrast, 'stable edges' should refer to situations where at least some populations have persisted *in situ* at suitable growing sites across Quaternary climatic oscillations, while the species expanded its range into other regions; these stable relict populations can be two or three orders of magnitude older than any populations from the rest of the range and have often persisted in long-term isolation. So far, opinions differ as to the relative importance of these two types of rear edges (Bennett *et al.* 1991; Davis & Shaw 2001), but phylogeographic surveys suggest that relict populations exist in a large number of species, particularly whenever mountain ranges are present at low latitudes of current ranges (e.g. Hewitt 2000, 2004; Petit *et al.* 2003). In what follows, we focus on 'stable' rear edges, given their importance for the conservation of species' biodiversity.

FEATURES OF STABLE REAR EDGE POPULATIONS

Such populations should occur mostly in regions that have provided suitable conditions for species persistence under both cold stage and warm stage conditions (Tzedakis *et al.* 2002). These regions typically harbour a heterogeneous topography, which allows populations to match suitable climatic conditions by relatively small altitudinal shifts. Under current climatic conditions, extant populations of terrestrial organisms are primarily constrained by water availability, while water temperature and its secondary effects are probably most limiting for aquatic and marine species. In either ecosystem, rear edge populations are typically restricted to particular habitat islands within a matrix of unsuitable landscapes. Figure 1 illustrates some of their most salient features. Rear edge populations are typically small and so isolated that regional population dynamics cannot easily compensate local extinction events. Their successful long-term persistence in spite of fairly small population sizes, at least during interglacial periods, indicates that extinction because of demographic stochasticity has played a relatively minor role (contradicting the centre-periphery-model). However, their small size and prolonged isolation have resulted in reduced within-population genetic diversity (see e.g. Castric & Bernatchez 2003; Petit *et al.* 2003; Chang *et al.* 2004). On the other hand, disproportionately high levels of genetic differentiation are observed among such populations, even between nearby ones, leading to exceptionally high levels of regional genetic diversity (Comps *et al.* 2001; Castric & Bernatchez 2003; Hampe *et al.* 2003; Petit *et al.* 2003; Martin & McKay 2004). Note indeed that most of these relict populations have not been the source of major postglacial recolonizations, contrary to common belief, thereby preserving their high genetic distinctiveness (e.g. Bilton *et al.* 1998; Petit *et al.* 2003). Furthermore, selection for local adaptation rather than for

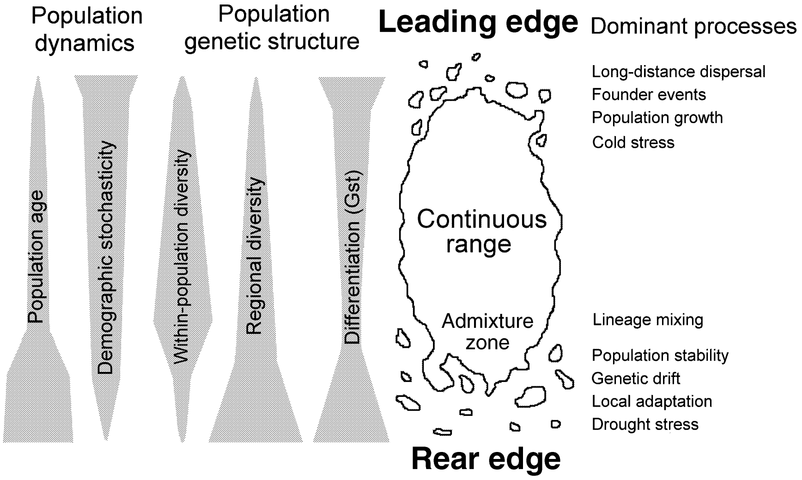

Figure 1 Population features and relevant processes at the leading and the rear edge of species ranges. The width of grey bars shown on the left hand indicates the quantity of features at the corresponding position within the range.

vagility and generalism is expected in these populations (Dynesius & Jansson 2000), which can, in association with reduced gene flow, result in the development of remarkably distinct ecotypes (Hampe & Bairlein 2000; Castric & Bernatchez 2003; Pérez-Tris *et al.* 2004).

LONG-TERM IMPORTANCE OF THE REAR EDGE

Present-day geographic patterns of biodiversity result from the interplay of three population-dynamic processes acting throughout the Quaternary: divergence (ultimately leading to speciation), extinction and migration. The description of migration processes during postglacial range expansions has been a major goal of palaeoecological and, more recently, phylogeographic research. However, patterns observed during interglacial periods have regularly been wiped out at their end, as range contractions have mostly resulted from massive population extinctions at high-latitude range margins, whereas migration towards lower latitudes has apparently been of little importance (Bennett *et al.* 1991; Jansson & Dynesius 2002). Consequently, patterns of migration should have had a minor effect on the evolution and maintenance of biodiversity across Quaternary climate oscillation.

In contrast to the individualistic nature of migration processes, Quaternary species extinctions have apparently been remarkably deterministic. Svenning (2003) showed recently, in a thorough analysis of the Northwest European Tertiary tree flora, that only the most climate-tolerant genera were able to cope with Quaternary climate oscillations, whereas cold-sensitive but relatively drought-tolerant genera are now restricted to the southern Mediterranean Basin and the least tolerant genera have completely disappeared from the continent (while they survived in the milder regions of North America and East Asia). This pattern underscores the importance of the long-term persistence of rear edge populations in shaping current biogeographical patterns through its mitigating effect on extinctions. It is probably not limited to temperate latitudes, as the regional richness of plant and vertebrate endemic species worldwide is positively correlated with past climate stability (Jansson 2003).

Rear edge populations should also have played a major role in the diversification of the biota. Many modern species of plants and animals date back to the Tertiary (Hewitt 2000; Willis *et al.* 2004). Since gradual speciation appears to be a slow process, at least in long-lived taxa, it would seem that only regions that have allowed long-term population persistence through both cold and warm Quaternary stages have some chance of giving birth to new species (Jansson & Dynesius 2002). In phylogeographic studies, only 'shallow' lineages are generally found at high latitudes compared with much deeper lineages in areas where survival under glacial maximum conditions is probable (Petit *et al.* 2003; Hewitt 2004). This negative relationship between lineage divergence and latitude is especially strong in regions that have been under the most direct influence of Quaternary glaciations, but it is not exclusive to this part of the globe (Martin & McKay 2004).

Hence, populations that inhabit present-day rear edges of species ranges appear to have played a key role for the maintenance of biodiversity throughout the Quaternary. A thorough evaluation of their current performance and viability appears therefore of utmost importance for successful conservation of intra- and interspecific biodiversity under anticipated global change.

RESEARCH ON REAR EDGE POPULATIONS

We conducted a bibliometric study to identify current trends in research on peripheral populations. The ISI Web of Science bibliographic database (1945 to October 2004) was screened in a heuristic search using the combined terms 'population', 'range' and 'margin', as well as different synonyms. (The combination was necessary to exclude studies from other disciplines and retain a manageable sample size.) Original studies that focused on global-scale range margins were considered only when they provided a minimum amount of ecological information, thereby excluding studies that merely reported new peripheral populations of a given taxon. Papers were classified according to the principal focus of the study (theoretical, genetic or ecological), their consideration or not of past or future dynamics and the type of study organism and ecosystem.

We found a total of 382 studies dealing with range margins, most of them published in recent years (Fig. 2). Most studies (86%) took place in terrestrial ecosystems (vs. 4% for aquatic and 5% for marine ecosystems). Latitudinal range margins were investigated in 300 papers, while the rest reported on other situations (mostly recent invasions, other core-periphery situations or modelling exercises). An increasing fraction of studies has considered the dynamic nature of species ranges, although it is still ignored in many recent investigations (Fig. 2). The vast majority of research has taken place in Europe or North America. There has been a strong bias towards high-latitude range margins (86% of studies), whereas only a relatively minor number of studies dealt with rear edge populations: 27 with static and 20 with dynamic range perspectives, plus 16 surveys that included both range margins. No theoretical or modelling exercise has so far explicitly explored the behaviour of rear edge populations, be they of the 'stable' or the 'trailing' type (Fig. 2; cf. Travis & Dytham 2004 for a related study). Likewise, no experimental work or long-term data series and very few palaeoecological analyses of the fossil record (but see Tzedakis *et al.* 2002) have focused on low-latitude range margins, in contrast to the opposite periphery. Virtually all

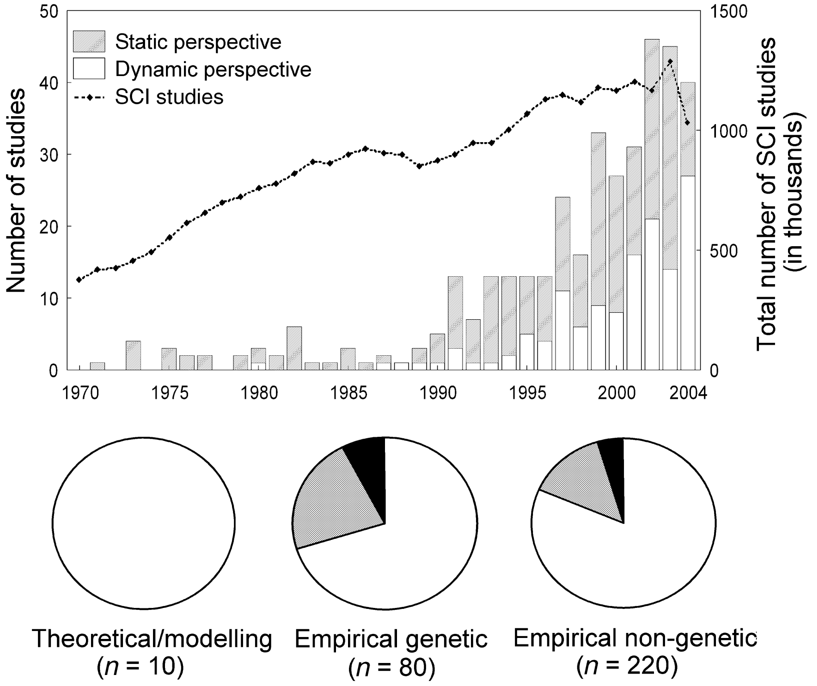

Figure 2 Development and main fields of research on peripheral populations. The upper graph illustrates the number of papers on this topic published annually since 1970, which are compared with the total number of publications included in the ISI Science Citation Index (SCI). Only those papers that had appeared in the SCI database by October 2004 are included (i.e. < 75% of the total for that year). Pie charts show the fraction of theoretical and different types of empirical studies that have been carried out at high-latitude (white), at low-latitude (black) and at both range margins (grey), respectively.

available information on rear edge population dynamics comes therefore from snapshot studies that have either been carried out along climatic gradients (e.g. García *et al.* 1999; Epps *et al.* 2004) or have extrapolated results of short-term studies on long-term series of weather data (e.g. Hódar *et al.* 2003; Hampe 2005). A range-dynamic view has largely remained the domain of phylogeographic research, while few ecological field studies have been designed to assess range dynamics at the rear edge (in stark contrast with range margins at high latitudes or altitudes). The earliest notable exception was Hamburg & Cogbill's (1988) investigation of the recent decline of red spruce (*Picea rubens* Sarg.) in the Eastern USA. Since then, an increasing number of studies have started to document and analyse recent altitudinal range shifts at the low-latitude range margin of species because of extinction of the lowermost populations (e.g. Parmesan 1996; Fisher 1997; Pounds *et al.* 1999; Peñuelas & Boada 2003; Epps *et al.* 2004; Lesica & McCune 2004).

PRESENT AND FUTURE PERFORMANCE OF REAR EDGE POPULATIONS

Virtually all field ecological research has been conducted on perennial plants. Studies have largely focused on reproduction and initial recruitment, as these are the most dynamic and variable stages of the regeneration cycle and therefore most amenable to short-term ecological studies. Negative effects of recent climate change on rear edge populations have been identified for the Eurasian shrub *Frangula alnus* Miller, whose seed production is greatly affected by the timing of the onset of summer drought, which has advanced significantly over the past few decades (Hampe 2005). In contrast, increasing winter temperatures appear to depress reproductive success in southern peripheral populations of *Pinus sylvestris* L., as they favour outbreaks of the pine processionary caterpillar, *Thaumetopoea pityocampa* Schiff (Hódar *et al.* 2003). Studies on initial plant recruitment have usually observed that water stress during summer reduces seedling survival to almost zero in the most peripheral populations, which appear to be virtually remnant under current climatic conditions (García *et al.* 1999; Peñuelas & Boada 2003; Castro *et al.* 2004). However, for long-lived organisms, demographic trends of rear edge populations cannot simply be inferred from their current recruitment rates (e.g. Eriksson 1996; Clark *et al.* 1999). Instead changes of adult mortalities could be much better indicators, but these have scarcely been monitored. A notable exception is the work of Allen & Breshears (1998) who reported a massive dieback of *P. ponderosa* Douglas ex Lawson & C. Lawson in a New Mexican woodland ecotone during a recent severe drought period. However, this case exemplifies a classical 'trailing edge' situation. Instead, the existence of stable rear edges could be particularly common in those plant or animal species whose populations are able to endure long periods without recruitment (by long life span, clonal growth, persistent seed banks etc.; cf. García & Zamora 2003). Unfortunately, too few empirical studies exist at present to test this hypothesis. Finally, it would be interesting to test if climate change affected rear edge population performance primarily through direct abiotic limitations, such as drought in terrestrial or water temperature in aquatic systems, or via their effects on biological interactions, such as competition or the breakup of mutualistic relationships (e.g. Loehle 1998).

Altogether, ecological research on rear edge populations is still very limited, making predictions hazardous. At the same time, predictions based on climate envelope modelling (e.g. Thomas *et al.* 2004) are becoming commonplace and these seem to leave little long-term prospects for rear edge populations, despite observations on the importance and historical continuity of many rear edge populations discussed in the preceding paragraphs. In fact, work on current impacts of global change indicates greater stability of low-latitude than of high-latitude range margins: for instance, during the 20th century, 34% of the non-migratory butterfly species surveyed by Parmesan *et al.* (1999) had stable high-latitude distribution edges compared with 72% that had stable low-latitude edges. The authors suggest that the greater average stability of low-latitude range limits is possibly not because of climatic factors but to biotic ones and to the heterogeneous topography in rear edge populations that offers a greater diversity of climatic 'niches'. It seems thus that (stable) rear edges might not disappear as readily as forecasted by bioclimate envelope models (e.g. Skov & Svenning 2004; Thomas *et al.* 2004). Indeed, such models make a number of unrealistic assumptions, particularly so for rear edge populations (Loehle & LeBlanc 1996; Loehle 1998; Thuiller *et al.* 2004). For instance, species' current ranges are assumed to be in equilibrium with their environment and to reflect primarily climatic tolerance, whereas other factors, such as dispersal limitation or interactions with other organisms, are often neglected (Iverson *et al.* 2004; Svenning & Skov 2004; Thomas *et al.* 2004). Perhaps most importantly in the context of rear edges, bioclimate envelope models rely mostly on climate data derived from global circulation models and ignore that regional-scale climate changes can be buffered locally by topographic heterogeneity. In summary, two visions of the future of rear edge populations currently coexist, ranging between predictions of complete disappearance based on modelling and more optimistic expectations based on past persistence. A more balanced view will probably emerge once more research will have been conducted on these populations.

RESEARCH AND CONSERVATION NEEDS

We are only beginning to understand the biological implications of past and ongoing range shifts on species' genetic constitution and evolutionary potential (e.g. Davis & Shaw 2001; Petit *et al.* 2004), and bridging both large-scale and local-scale perspectives is required to appreciate the character and conservation needs of rear edge populations, a difficult exercise. Palaeoecological studies are usually of little help, as their geographical resolution is generally too coarse to detect the historical existence of small relict populations. Furthermore, 'relict hotspots' – areas that harbour rear edge populations of many species – are commonly located in regions of the world where the socio-economic situation limits research activities. As these relict hotspots often coincide with centres of high biodiversity and endemism, other organisms will often have monopolized most resources. Accordingly, the value of relict populations at the low-latitude margins of many species' distribution ranges has remained largely unperceived by conservation biologists. Some glacial relicts have been included in regional or national red lists, but neither research nor conservation programs seem to have been dedicated to rear edge populations *per se* (although Lesica & Allendorf (1995) have considered the conservation value of peripheral populations in general). Here, we outline three areas in which further development of research and conservation measures appears particularly necessary.

(1) Exploratory surveys should identify further centres of relict diversity. Outside Europe and North America our knowledge about the location of glacial refugia is still very fragmentary (Noss 2001; Hewitt 2004). Relicts hotspots should be concentrated in a limited number of regions around the globe that have allowed survival of many species during both Quaternary cold and warm stages in particular wet and/or cool habitats. The typically small size of these sites should render their detection difficult but could facilitate subsequent conservation measures. On the other hand, it makes them prone to human disturbance, particularly in arid regions where human water demands and browsing by cattle represent serious threats (e.g. Danin 1999; García *et al.* 1999).

(2) The performance of rear edge populations under changing environmental conditions should become a focus of interdisciplinary research, by integrating demographic and genetic work with modelling approaches and with community ecology. So far, almost all research has focused on temperate perennial plants, and investigation of a broader spectrum of organisms, communities and biomes is clearly needed. Long-term experimental studies are required that distinguish climate effects from other factors, such as habitat fragmentation, genetic load in small populations or biotic interactions. For instance, competition with surrounding communities (or invasive aliens) appears to accelerate the breakdown of 'islands' of relict vegetation (Pounds *et al.* 1999; Peñuelas & Boada

2003), which might otherwise be more resistant to direct climate effects. However, species interactions could also have the opposite effect, since facilitation tends to increase under water stress (cf. Danin 1999; Castro *et al.* 2004), allowing persistence of a given species in areas where simple models predict that it cannot survive. Realistic predictions of future rear edge population performance requires the development of models that can integrate population dynamics, ecosystem processes and climate trends at landscape to regional scales (Hannah *et al.* 2002).

(3) Appropriate conservation strategies need to be designed that consider the peculiarities of rear edge populations. For instance, the particular genetic structure of rear edge populations requires conservation strategies directed towards the detection and maintenance of the greatest possible number of local populations, regardless of their size or performance, instead of focusing on the most viable core populations. Likewise, improvement of landscape connectivity is commonly considered essential to allow species to match climate changes by shifting their range (e.g. Noss 2001; Hannah *et al.* 2002; Thomas *et al.* 2004), but it would be of little use at stable rear edges and might even be counterproductive, if it enhances competition with surrounding communities or promotes invasion by aliens. Hence, specific conservation measures will have to be identified to effectively preserve these relict populations.

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When Are Peripheral Populations Valuable for Conservation?

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When Are Peripheral Populations Valuable for Conservation?

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Abstract: *A great deal of effort is spent protecting geographically peripheral populations of widespread species. We consider under what conditions it is appropriate to expend resources to protect these populations. The conservation value of peripheral populations depends upon their genetic divergence from other conspecific populations. Peripheral populations are expected to diverge from central populations as a result of the interwoven effects of isolation, genetic drift, and natural selection. Available empirical evidence suggests that peripheral populations are often genetically and morphologically divergent from central populations. The long-term conservation of species is likely to depend upon the protection of genetically distinct populations. In addition, peripheral populations are potentially important sites of future speciation events. Under some circumstances, conservation of peripheral populations may be beneficial to the protection of the evolutionary process and the environmental systems that are likely to generate future evolutionary diversity.*

¿Cuándo resultan las poblaciones periféricas valiosas para la conservación?

Resumen: *Se gasta mucho esfuerzo protegiendo poblaciones geográficamente periféricas de especies ampliamente distribuidas. En el presente estudio, consideramos bajo que condiciones es apropiado gastar recursos para proteger estas poblaciones. El valor de conservación de las poblaciones periféricas depende de su divergencia genética con respecto a otras poblaciones de la misma especie. Se espera que las poblaciones periféricas diverjan de poblaciones centrales como resultado de los efectos interconectados del aislamiento, la deriva genética y la selección natural. Evidencia empírica disponible sugiere que las poblaciones periféricas son con frecuencia, divergentes genética y morfológicamente de las poblaciones centrales. La conservación a largo plazo de las especies depende probablemente de la protección de las poblaciones genéticamente distintas. Adicionalmente, las poblaciones periféricas son potencialmente importantes para eventos de especiación futuros. Bajo algunas circunstancias, la conservación de poblaciones periféricas podría ser beneficiosa para la protección de los procesos evolutivos y sistemas ambientales que probablemente generen la diversidad evolutiva futura.*

Introduction

Geographically peripheral populations are more likely to be imperiled than central populations. They tend to occur in less suitable environments and are often isolated from more central and continuous populations. Thus, peripheral populations are often smaller and more prone to extirpation due to stochastic or catastrophic demographic events.

Some authors have distinguished between geographically marginal (peripheral) populations and ecologically marginal populations (Shumaker & Babble 1980; Soulé 1973). Strictly speaking, peripheral populations are separated from central ones by spatial distance, while ecologically marginal populations experience different biotic or abiotic environments. In many cases, however, peripheral populations are also ecologically marginal. In our discussion, peripheral populations are always geo-

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graphically marginal and may be ecologically marginal as well.

A great deal of effort and resources are spent protecting peripheral populations of widespread species. Protection of peripheral populations is often linked to political boundaries. The American sycamore (*Platanus occidentalis*) is listed as threatened in Wisconsin by the Wisconsin Department of Natural Resources, even though it is common in Illinois and further south and east (Read 1976). *Iris missouriensis* occurs throughout much of western North America but is listed as rare in Alberta and British Columbia at the northern edge of its range (Packer & Bradley 1984; Straley et al. 1985) and is given conservation priority status 1 in Canada (Argus & Pryer 1990).

The Nature Conservancy in the U.S. assigns conservation priorities on both global and state levels. Globally endangered elements receive top priority, but those with high state ranks also receive considerable attention. Federal land-management agencies also provide protection to peripherally rare plants. *Mertensia bella* is listed as sensitive in the northern region of the U.S. Forest Service, even though the species is more common further west (Reel et al. 1989). These sorts of programs allow nations, states, and provinces to protect biological diversity within their political boundaries.

Is it wise to spend limited conservation resources on protecting populations of a species that happens to be rare within a politically defined geographical area but that is globally secure? We consider biological reasons for protecting peripheral populations when the species is secure in the center of its range—that is, when peripheral populations are important for the evolutionary future of species by increasing their ability to evolve new adaptations.

We also consider the potential value of peripheral populations as a source of future speciation events. Evolution occurs by changes within a single evolutionary lineage (anagenesis) and the branching of a single lineage into multiple lineages (cladogenesis). Some authors consider peripheral populations an important source of future speciation events. Thus, conservation of peripheral populations may be beneficial to the protection of the evolutionary process and the environmental systems that are likely to generate future evolutionary diversity.

We review relevant theoretical and empirical literature dealing with the population biology of peripheral populations and suggest why and when they are likely to be valuable for conservation. In some cases, species at the edge of their range may play a keystone role in the ecosystem. These ecological values are obviously important, but they are beyond the scope of this paper. We have drawn upon the plant literature for empirical data, but the principles that emerge are applicable to animals as well. A discussion of the importance of marginal populations of fish has been presented by Scudder (1989).

Theoretical Considerations

Peripheral populations will diverge from central populations as a result of two interwoven processes: genetic drift and natural selection. The isolation and smaller size of peripheral populations should lead to less genetic variation than in central populations because of genetic drift. The effects of natural selection on the amount of genetic variation in peripheral populations is less predictable.

Peripheral populations occur near the outer boundary of the geographic range of the species and are often relatively small and isolated from central populations (Mayr 1963; Levin 1970; Lawton 1993), and consequently gene flow will be reduced. Furthermore, outlying populations are often founded by only a small number of individuals, and this can result in a significant reduction in multilocus heterozygosity and allelic variation (Nei et al. 1975; Allendorf 1986; McCommas & Bryant 1990). Reduced gene flow (isolation), small population size, and founder effects will all promote genetic drift and result in reduced genetic variation and increased differentiation of peripheral populations.

Peripheral populations are likely to experience different regimes of natural selection than central populations. Environmental factors often change in a clinal manner (Endler 1977). Presumably, central populations experience the most favorable environmental conditions, and environmental favorableness decreases with distance from the center (Lawton 1993). Thus, geographic outliers are likely to occur in ecologically marginal or stressful conditions. But conditions at the species boundary are likely to be different even if they are not less favorable. Many species at the edge of their range occur in unusual or atypical habitats (Fernald 1925; Gankin & Major 1964). Thus, peripheral populations are expected to be genetically distinct because of divergent natural selection.

In addition, even similar selective pressures may lead to increased genetic divergence of peripheral populations because of their isolation (Cohan 1984; Cohan & Hoffman 1986; Hoffman & Cohan 1987). Selection with drift in isolated populations may result in greater divergence than either selection or drift alone (Cohan & Hoffman 1986). Cohan (1984) reviewed examples of natural populations of plants and animals that have diverged under similar directional selection pressures.

There is some evidence that heterozygous advantage is more pronounced in populations in marginal environmental conditions (reviewed in Lesica & Allendorf 1992). Thus, intensified heterozygous advantage in peripheral populations under environmentally marginal conditions may act to maintain more genetic variation at some loci than would be expected on the basis of the reduced population size alone. In general, however, we would expect genetic variation to be less in peripheral populations.

Thus, the two primary factors affecting the distribution of genetic variation within a species, genetic drift and natural selection, are both expected individually to promote divergence of peripheral populations. Acting in concert, genetic drift and natural selection may have synergistic effects. For example, many authors believe that population bottlenecks often result in genetic reorganization by breaking down coadapted gene complexes (Mayr 1963; Lewis 1966; Levin 1970; Carson 1975; Templeton 1980). Restricted gene flow and directional selection enhance this process (but see Barton & Charlesworth 1984). Bottlenecks, restricted gene flow, and novel selection regimes are all more likely in peripheral populations.

Empirical Results

Peripheral populations may have reduced genetic variation compared to central populations, but this is not always the case. Numerous studies of plants have compared multilocus heterozygosity between central and peripheral populations using enzyme electrophoresis. Peripheral populations showed reduced genetic variation compared to central populations in conifers such as *Chamaecyparis lawsonii* (Millar & Marshall 1992), *Pinus contorta* (Yeh & Layton 1979; Cwynar & MacDonald 1987), *P. jeffreyi* (Furnier & Adams 1986), *P. ponderosa* (Hamrick et al. 1989), and *P. rigida* (Guries & Ledig 1982); in deciduous trees such as *Betula* (Coyle et al. 1982) and *Gleditsia* (Schnabel & Hamrick 1990); and in herbaceous species including *Avena* (Jain et al. 1981), *Chenopodium* (Crawford & Wilson 1977), *Hordeum* (Shumaker & Babbel 1980), *Limnanthes* (Arroyo 1973*b*), *Lycopersicon* (Rick et al. 1977), *Lysimachia* (Agnew 1968), and *Sarracenia* (Schwaegerle & Schaal 1979). However, examination of peripheral populations of *Picea abies* (Tigerstedt 1973), *Pinus edulis* (Betancourt et al. 1991), *Pseudotsuga menziesii* (Yeh & O'Malley 1980), *Camelia japonica* (Wendel & Parks 1985), and *Phlox* spp. (Levin 1977, 1978) did not reveal reduced genetic variation compared to central populations.

Founder effects and drift due to reduced gene flow should cause peripheral populations to have different alleles or gene frequencies than central populations. Studies of gene frequencies using enzyme electrophoresis have detected such differences in many plant species, including *Chamaecyparis lawsonii* (Millar & Marshall 1992), *Eucalyptus caesia* (Moran & Hopper 1983), *Pinus contorta* (Wheeler & Guries 1982), *P. edulis* (Betancourt et al. 1991), *P. jeffreyi* (Furnier & Adams 1986), *P. ponderosa* (Mitton et al. 1980; Hamrick et al. 1989), *P. radiata* (Moran et al. 1988), *Chenopodium fremontii* (Crawford & Wilson 1977), *Hordeum jubatum* (Shumaker & Babbel 1980), and *Lycopersicon pimpinellifolium* (Rick et al. 1977).

Divergence between populations may also occur through repatterning of chromosomes. Structural rearrangements (such as inversions and translocations) initially result in greatly reduced fertility. Individuals carrying such rearrangements have little chance of contributing to the following generation in large, central populations, but they can become established in small, isolated peripheral populations (Lewis 1966). Lewis (1962, 1966), Grant (1981), and James (1965) provide examples of chromosome repatterning in peripheral populations in *Clarkia, Gilia,* and *Isotoma*, respectively. Although these peripheral populations may be morphologically similar to central populations (Lewis 1966), they are usually isolated reproductively and constitute a unique evolutionary unit. Repatterning may be accompanied by reduction in chromosome number (Stebbins 1950). The formation of novel hybrids and allopolyploids is thought to be favored by the presence of ecologically marginal habitats (Anderson 1948; Stebbins 1950, 1959; Johnson et al. 1965). Peripheral populations often encounter such habitats.

Morphological (quantitative) characters are expected to diverge more rapidly in isolated populations than are gene frequencies detected by electrophoresis (Lewontin 1984; Helenurm & Ganders 1985; Lowry & Crawford 1985, Crawford et al. 1987; Crawford & Whitkus 1988; Witter & Carr 1988). Consequently, we expect that divergence associated with geographic isolation will be more manifest in quantitative characters (Merrell 1981; Schwaegerle et al. 1986). Populations of *Pinus contorta* near the northern boundary of its range show significant differences in seed size and shape associated with selection for dispersal capability (Cwynar & MacDonald 1987). Monoecious forms of the widespread prairie grass *Buchloe dactyloides* are more common in peripheral populations (Huff & Wu 1992). In both *Lasthenia* (Ornduff 1966) and *Leavenworthia* (Solbrig & Rollins 1977), self-fertilizing populations occur at the geographic periphery of outcrossing species or species complexes. Ornduff (1966) found that the highest concentration of morphological variants in many species of *Lasthenia* occurred near the margin of their geographical range. Peripheral populations with deviant morphological characters are common in many species of *Clarkia* (Lewis & Lewis 1955), and isolated, morphologically distinct races have been reported for a number of species of *Gilia* (Grant & Grant 1956). The systematics literature provides numerous examples of morphological differentiation of peripheral populations.

Conservation Value

It is widely acknowledged that species conservation depends upon protecting the genetic variability present throughout the range of the species. Ehrlich (1988) has argued that "The loss of genetically distinct populations within species is, at the moment, at least as important a problem as the loss of entire species." Environments continually change; to survive, organisms must have genetic variability that allow them to evolve (Frankel & Soulé 1981; Beardmore 1983; Gilpin & Soulé 1986). Genetic variation is partitioned within and among populations. Preserving the within-population component involves protecting large viable populations (central populations) that will not lose variation due to drift (Lande & Barrowclough 1987).

An important method for conserving the among-populations component of genetic variation is to protect the most genetically distinct populations (Millar & Libby 1991). Numerous authors have emphasized that more-divergent taxa or populations have greater conservation value (May 1990; Van-Wright et al. 1991; Brooks et al. 1992; Crozier 1992; Faith 1992; Holsinger 1992). Available evidence suggests that peripheral populations are often genetically and morphologically divergent from central populations. Distinct traits found in peripheral populations may be crucial to the species, allowing adaptation in the face of environmental change. We do not mean to imply that only peripheral populations are important but only that they are often disproportionately important for protecting genetic diversity relative to their size and frequency.

Many consider the species periphery one the most active regions of speciation (Simpson 1944; Mayr 1954, 1963; Carson 1959; Stebbins & Major 1965; Levin 1970, 1993). Thus, peripheral populations may often be important for the survival and evolution of species and will often have high value for conservation.

It is the degree of drift and intensity of selection that determine the amount of genetic divergence and conservation value of peripheral populations. A simplified scheme illustrating this relationship is presented in Figure 1. An analogous framework for determining conservation value has been presented by Dizon et al. (1992). There are a variety of factors likely to affect the amount of drift and the intensity of natural selection. All of these will have some effect on the amount of divergence between peripheral and central populations and may have antagonistic or synergistic effects. In particular cases any one factor may be of overriding importance.

(1) Spatial Distance

Gene flow to peripheral populations will be reduced in proportion to their degree of isolation. In those species with relatively few, widely dispersed outliers, peripheral populations should be more divergent from central populations. In other words, the more disjunct the populations are, the more divergent they are likely to be. Northern peripheral populations of *Pinus contorta* are smaller and more isolated than those further south and also have more strongly differentiated gene pools (Cwynar & MacDonald 1987; Yeh et al. 1985). Reduced gene flow will lower the swamping effect from larger central populations and promote changes in the frequency of neutral or near-neutral alleles (drift) or alleles that are being selected in a novel environment.

(2) Life History

Species with life-history attributes that cause reduced gene flow are also more likely to form evolutionarily significant peripheral populations for the same reasons given above. Plants with limited pollen and seed dispersal should have reduced gene flow compared to more vagile species. In addition, species experiencing a high proportion of self-fertilization should also have reduced gene flow. Conifers that have widely dispersed pollen and seed and maintain a high level of outcrossing generally have low levels of interpopulation differentiation (Hamrick 1983). Diversification rates are lower for plant families made up predominantly of wind-pollinated members (Eriksson & Bremer 1992). Selfing species, however, have a high percentage of their genetic variation partitioned among populations (Usberti & Jain 1978; Hamrick 1983).

Species with low fecundity will regain population size more slowly following a founder event. As a result, they will suffer a greater loss of genetic variation than species able to quickly recover large populations (Nei et al. 1975). A significant loss in variation could precipitate a

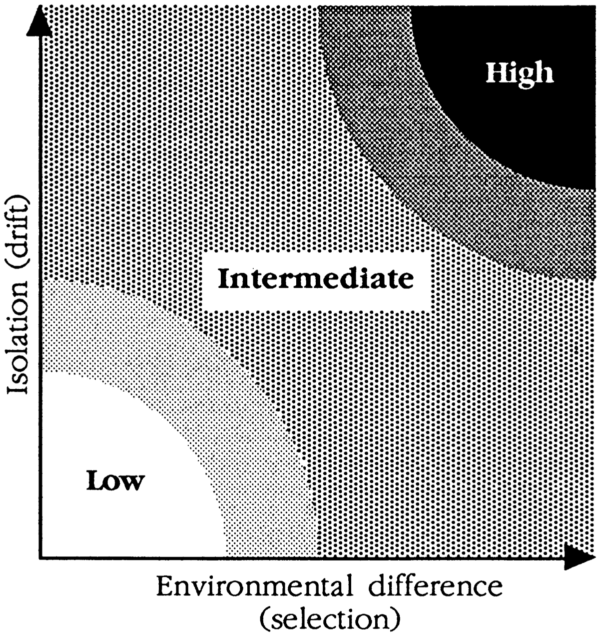

Figure 1. Relative conservation value of peripheral populations from an evolutionary perspective.

reorganization of linkage groups and could lead to genetic divergence in peripheral populations (Mayr 1963; Lewis 1966; Grant 1981).

(3) Time

Generation time may also play a role in the divergence of isolated populations (Niklas et al. 1985). Species with shorter generation times will diverge more quickly during the same length of time. Shorter generation time has been used to explain the fact that there are many more small species than large (Stebbins 1950; Simpson 1953; Van Valen 1973). There is evidence for divergence of peripheral populations in many groups of annuals such as *Clarkia* (Lewis 1966), *Gilia* (Grant & Grant 1956), *Lasthenia* (Ornduff 1966), *Limnanthes* (Arroyo 1973*a*, 1973*b*), and *Stephanomeria* (Gottlieb 1973). Because many annuals are also self-pollinating, it is not always possible to separate the effects of generation time from breeding system. Shorter generation times will speed up rates of differentiation due to both drift and natural selection.

In species for which there has been a recent expansion or contraction of geographic range, peripheral populations will not usually have had enough time to become divergent due to selection or drift. This includes species that recently have undergone habitat reductions due to human actions. Populations that became disjunct during the Altithermal period (about 7000 years ago) should be less divergent than those separated during the Pleistocene (more than 10,000 years ago). Often this factor cannot be determined.

(4) Ecological

Directional selection can be a strong force causing the divergence of peripheral populations. Selection regimes will be most effective at causing divergence when peripheral populations occupy habitats that are very different or more stressful from those in the center of the range. Population differentiation can be associated with differences in soils (Snaydon & Davies 1982; Heywood & Levin 1985; Macnair 1987), fire frequency (Ledig & Fryer 1972), and climate (Clausen et al. 1948; Bradshaw 1960). Divergence may also result from differences in biotic environment such as competitors (Grant & Antonovics 1978; Turkington & Aarssen 1984), pollinators (Grant & Grant 1965; Feinsinger 1983), dispensers (Carlquist 1966; Helenurm & Ganders 1985) or pests (Futuyma 1983). Because ecological changes are often clinal, spatial separation and ecological divergence will frequently be correlated, and more isolated populations will often be more divergent.

Spatial isolation, poor dispersal ability, short generation time, and ecological distance will all promote genetic differentiation and the likelihood of genetic divergence. Although our findings do not lend themselves to hard and fast rules for constructing priorities, in many cases they can be helpful in guiding conservation decisions. For example, *Carex chordorhiza* is a circumboreal sedge with a number of peripheral populations in northwest Montana and adjacent Idaho. There is a single population disjunct 200 km to the south that is more likely to a have unique gene pool than the other peripheral populations. *Thelypteris phegopteris* is a widespread boreal fern, found in acid soil of cliffs and forests (Lellinger 1985). At the southern edge of its range in northwest Montana, *T. phegopteris* occurs at seven sites. Six are in mesic coniferous forests, and the other is on subalpine calcareous cliffs. The second site is most likely to have a divergent genotype and should be given conservation priority.

Protecting biological diversity in the face of accelerating human-caused perturbations is a major undertaking. In many cases, broad community or landscape approaches may be most efficient (Noss 1987; Franklin 1993). Nonetheless, the "fine-filter approach" of protecting endangered species, subspecies, and populations is an important complement to more large-scale efforts (Franklin 1993), especially for maintaining the genetic variability of species (Millar & Marshall 1992). Protection of peripheral populations is currently included in protection plans for economically important species (Millar & Libby 1992) and endangered species (Hickey et al. 1991; Ryttari & Lahti 1992) and can also be important for conserving the evolutionary potential of more widespread species. But not all peripheral populations are likely to be genetically divergent. Populations that have become isolated due to relatively recent range contractions or peripheral populations close enough to central populations that gene flow precludes genetic differentiation are not likely to be distinct. Thus, it is important to evaluate the conservation value of peripheral populations before expending resources on their protection.

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California Energy Resources Conservation
and Development Commission

In the Matter of: APPLICATION FOR CERTIFICATION FOR THE IVANPAH SOLAR ELECTRIC GENERATING SYSTEM	DOCKET NO. 07-AFC-5

DECLARATION OF SERVICE

I, Greg Suba, declare that on January 4, 2010, I served and filed copies of the attached Additional Exhibits #1009-1011 for Rebuttal Testimony of Intervenor California Native Plant Society, dated January 4, 2010. The original document, filed with the Docket Unit, is accompanied by a copy of the most recent Proof of Service list, located on the web page for this project at: www.energy.ca.gov/sitingcases/ivanpah]. The document has been sent to the other parties in this proceeding (as shown on the Proof of Service list) and to the Commission's Docket Unit, in the following manner:

(Check all that Apply)
FOR SERVICE TO ALL OTHER PARTIES:

__X__ sent electronically to all email addresses on the Proof of Service list;
__X__ by personal delivery or by depositing in the United States mail at with first-class postage thereon fully prepaid and addressed as provided on the Proof of Service list above to those addresses NOT marked "email preferred."
AND

FOR FILING WITH THE ENERGY COMMISSION:
__X__ sending an original paper copy and one electronic copy, mailed and emailed respectively, to the address below (preferred method);
OR
_____ depositing in the mail an original and 12 paper copies, as follows:

CALIFORNIA ENERGY COMMISSION
Attn: Docket No.
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Sacramento, CA 95814-5512
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I declare under penalty of perjury that the foregoing is true and correct.

Greg Suba
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