LETTER

# Favorable environments and the persistence of naturally rare species

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## Abstract

In an era of rapid climate change, it is important to understand how naturally rare species—such as those with small geographic ranges, specialized habitat requirements, and low local abundances—have persisted in time and space. In the flora we studied, species with all three forms of rarity inhabited geographic regions with more benign climates (higher total and summer rainfall, less extreme seasonal temperatures) and larger areas of their specialized habitat within 10 km than did more common species in the same habitats. Similar differences were also seen in congener-only comparisons. We found no evidence for two nonexclusive alternatives, that naturally rare species had more extinction-resistant life history traits, or that they belonged to more rapidly speciating taxa than common species. Understanding the association of rare species with benign environments may help in the design of effective conservation strategies for geographic regions of high diversity and endemism under changing climates. In particular, our findings highlight the extra climatic sensitivities of rare species with edaphic or other specialization, and how the needs of these species may be met by either refugia or translocation strategies.

## Introduction

Rare species are of considerable interest both because of their contribution to the Earth's biodiversity (Myers *et al*. 2000; Stein *et al.* 2000), and because they face high risk of extinction (Mace & Lande 1991). The resulting concern for rare species has led to efforts to identify biological traits that distinguish them from common species (Kruckeberg & Rabinowitz 1985; Kunin & Gaston 1993; Gaston & Kunin 1997). These studies have typically focused on the intrinsic traits of species, and have tended to identify differences that might be regarded as causing or contributing to rarity: for example, poorer dispersal, lower reproductive investment, lower genetic variation, lower competitive ability, higher susceptibility to pathogens, larger body sizes (in animals), and not surprisingly, higher degrees of habitat specialization in rare compared with common species (e.g., Kruckeberg & Rabinowitz 1985; Kunin & Gaston 1993; Gaston & Kunin 1997; Hegde & Ellstrand 1999; Bruno 2002; Klironomos 2002; Murray *et al.* 2002; Pilgrim *et al.* 2004; Kelly & Woodward 2005). In contrast, few consistent rare-common differences have been identified that are favorable to the persistence of rare species, one important exception being the tendencies toward higher asexuality and/or self-compatibility in rare compared to common plants (Kunin & Gaston 1993; Gaston & Kunin 1997).

Rare species are nonetheless frequent in most biotas, as ecologists have long known (Preston 1948). Rarity is often defined using the framework of Rabinowitz *et al.*(1986), which considers the three axes of range size, habitat specialism, and local abundance. In the British flora, Rabinowitz *et al.* (1986) found these three axes to be independent, habitat specialism to be the most frequent form of rarity, and relatively few species to be rare on all three axes. However, the same patterns are not found in all biotas (Schoener 1987; Ricklefs 2000). Many studies have found positive associations between range size and local abundance (Hanski 1982; Brown 1984), and studies that consider all three rarity axes often find high proportions of species that are rare in all three respects. For example, Yu & Dobson (2000) found 27% of a global sample of mammals had small ranges, were habitat specialists, and were locally sparse. These traits also held true for 27% of plants and 29% of amphibians and reptiles found in ecoregional Floridian sand pine scrub (McCoy & Mushinsky 1992).

The high frequency of rarity leads to the question of how naturally rare species have persisted through evolutionary time, and whether particular characteristics have enabled them to avoid extinction in spite of their small ranges, low abundances, and narrow habitat requirements. Here we ask whether naturally rare species are distinguished by their environmental, as opposed to their intrinsic, characteristics. For example, are they found in less-extreme climates (Yu & Dobson 2000) or in larger or less-fragmented areas of habitat (Fagan *et al.* 2005), or both? This is an important, nonexclusive alternative to the hypothesis that naturally rare species tend to have life history traits that confer extinction resistance. Another nonexclusive possibility is that naturally rare species actually do go extinct more frequently than nonrare ones over evolutionary time, implying that they should be younger on average and more likely to belong to rapidly speciating lineages than common species (Cowling *et al.* 1996; Chown 1997; Gavrilets *et al.* 2000; Schwartz & Simberloff 2001). These will be referred to for simplicity as the favorable-environment hypothesis, the intrinsic-trait hypothesis, and the rapid-speciation hypothesis.

We tested the favorable-environment hypothesis using a data set for plant species found on serpentine soils in California. Since the hypothesis applies only to natural (i.e., non-anthropogenically induced) rarity, an advantage of the serpentine flora is that a high proportion of its species can be considered to be naturally rare (although many naturally rare serpentine endemics have nonetheless received Federal or State threatened or endangered species designations; Safford *et al.* 2005). Some 246 plant taxa are restricted to serpentine in California, and these are, by definition, habitat specialists; most of them have substantially smaller ranges than other species in California (Harrison & Inouye 2002; Safford *et al.* 2005), and this is considered to be a natural phenomenon (Stebbins & Major 1965; Kruckeberg 1984; Raven & Axelrod 1978.) To measure local abundance, we used field sampling in locations that were not affected by visible impacts such as logging, mining, road building, urbanization, or recent fires (Harrison *et al.* 2006a). Serpentine soils are much less invaded than most other terrestrial habitats, and no impacts of exotic species on native species richness were detectable in our study (Harrison *et al.* 2006b).

We identified the "triply rare" (small range, habitat specialist, low abundance) species within this flora, and asked whether they inhabited more benign climates (higher total and summer rainfall, lower summer maximum temperatures, higher winter minimum temperatures), or were found in regions containing larger areas of their specialized habitat, as compared with all other species in the flora. We repeated this comparison using triply rare species and their congeners to determine whether any patterns we found were associated with differences among genera versus among species within genera (Kunin & Gaston 1993; Murray *et al.* 2002; Kelly & Woodward 2005).

We lacked adequate data for full tests of either the intrinsic-trait hypothesis or the rapid-speciation hypothesis. However, based on the traits for which we had data, we compared the triply rare species with others in terms of their life forms (perennial/annual, woody/herbaceous). One possibility is that rare species will tend to be perennial and/or woody (Hegde & Ellstrand 1999) because this may confer greater resistance to stochastic extinction; however, it has also been proposed that rare plants in Mediterranean climates tend to be annuals because short lifespans are conducive to rapid speciation (Cowling *et al.* 1996). To examine the rapid-speciation hypothesis, we asked whether triply rare species were more likely than others to belong to genera that are believed to have undergone rapid recent speciation (Raven & Axelrod 1978).

## Methods

### Study system and data collection

Serpentine or ultramafic rocks produce soils that contain high levels of magnesium and low concentrations of calcium and primary nutrients. Of the more than 5,000 native species in California, about 1,400 are tolerant of serpentine, including 246 taxa that are strictly specialized (endemic) to the substratum (Kruckeberg 1984; Safford *et al.* 2005; Harrison *et al.* 2006a). Using a geographically structured design, we sampled species occurrences in 109 field sites (each 1,000 $m^2$) in serpentine woodlands, chaparral, grasslands, and barrens throughout California over 4 years (see Figure 1 for a map of serpentine outcrops and study localities, and Harrison *et al.* 2006a for complete details on the assembly of the database.) As noted above, we avoided any sites with obvious signs of human disturbance. Each sampling site included two $50 \times 10$ m plots, paired for north and south slope exposure. Each plot contained seven $1 \times 1$ m subplots, within

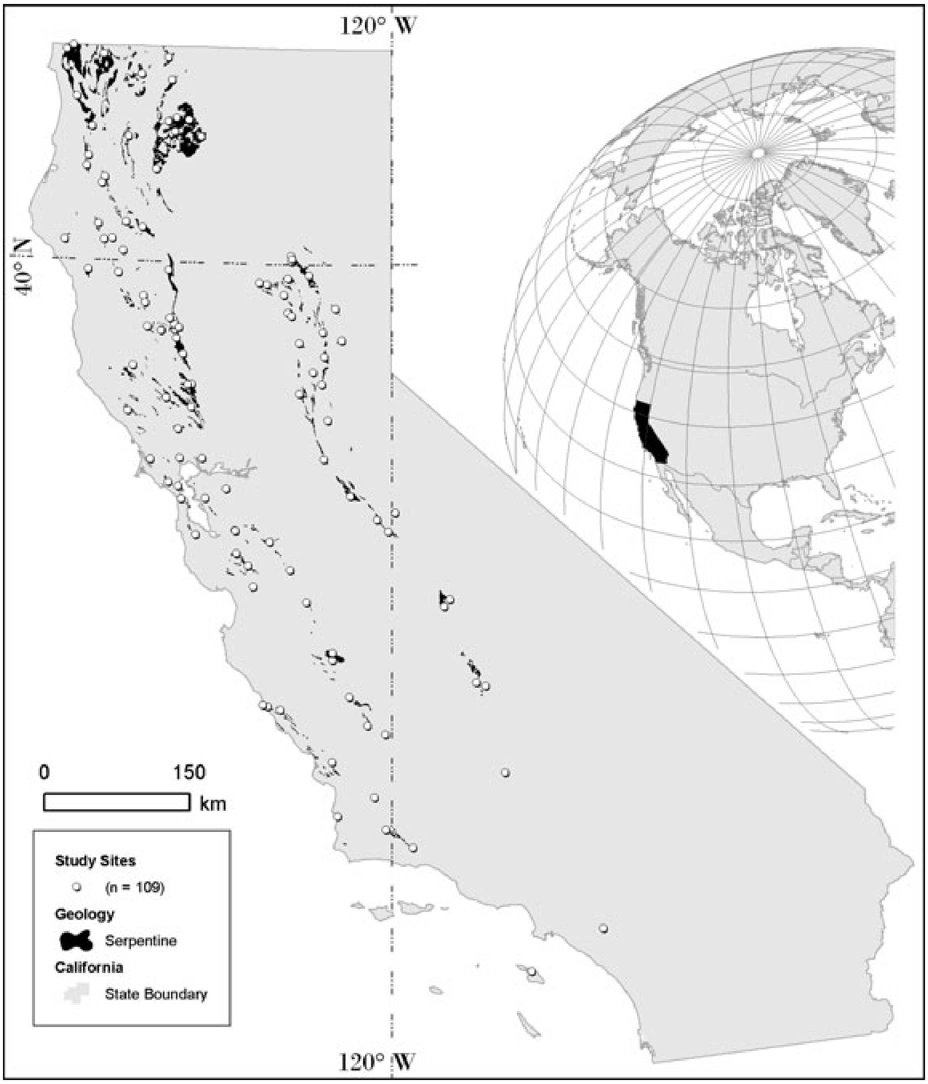

**Figure 1** Distribution of serpentine outcrops and study sites.

which we recorded percentage cover by each herbaceous species. We recorded woody species identity and cover along a central 50-m transect in each plot. For each herb species at each site we averaged its cover values in the 14 subplots, and for each woody species we averaged its cover values on the two transects, yielding one cover value per species per site.

For each of the 939 species we found, range sizes were obtained from Viers *et al.* (2006). The status of each species as a habitat specialist (serpentine endemic) or not was determined using an extensive review of literature and herbarium records by Safford *et al.* (2005). To measure local abundance, a mean cover value was obtained by averaging cover values across all sites where each species was found. Cover values are an imperfect surrogate for local abundance, and for some of the species that are not habitat specialists, cover values might be expected to be lower on serpentine than on other soils. However, both of these factors should, if anything, make it less likely that the data would confirm our prediction that locally sparse, small-range, habitat specialists will be found in more favorable environments than all other species.

## Classifying species

Only 73 (8%) of the 939 species we found were strict habitat specialists according to Safford *et al.* (2005). For

**Table 1** Triply rare species identified in this study

| Species | Family | Life form | Status |
|---|---|---|---|
| *Allium hoffmani* | Liliaceae | Herb | R |
| *Balsamorhiza sericea* | Asteraceae | Herb | R |
| *Calochortus obispoensis* | Liliaceae | Herb | R |
| *Campanula griffini* | Campanulaceae | Herb | — |
| *Carex obispoensis* | Cyperaceae | Herb | R |
| *Caulanthus amplexicaulis* | Brassicaceae | Herb | — |
| *Centaurium trichanthum* | Gentianaceae | Herb | — |
| *Chorizanthe breweri* | Polygonaceae | Herb | R |
| *Chorizanthe ventricosa* | Polygonaceae | Herb | R |
| *Collinisia greenei* | Polemoniaceae | Herb | — |
| *Cryptantha hispidula* | Boraginaceae | Herb | — |
| *Cryptantha mariposae* | Boraginaceae | Herb | R |
| *Dudleya setchelli* | Crassulaceae | Herb | E |
| *Ericameria ophiditis* | Asteraceae | Shrub | R |
| *Erigeron angustatus* | Asteraceae | Herb | R |
| *Erigeron bloomeri* | Asteraceae | Herb | — |
| *Eriogonum congdonii* | Polygonaceae | Shrub | R |
| *Eriogonum pendulum* | Polygonaceae | Herb | R |
| *Eriogonum tripodum* | Polygonaceae | Shrub | R |
| *Garrya congdonii* | Garryaceae | Shrub | — |
| *Hesperolinon congestum* | Linaceae | Herb | T |
| *Hesperolinon tehamense* | Linaceae | Herb | R |
| *Lagophylla minor* | Asteraceae | Herb | — |
| *Lomatium ciliolatum* | Apiaceae | Herb | — |
| *Monardella folletti* | Lamiaceae | Herb | R |
| *Nemacladus montanus* | Campanulaceae | Herb | — |
| *Polystichum lemmoni* | Pteridaceae | Herb | — |
| *Sedum albomarginatum* | Crassulaceae | Herb | R |
| *Streptanthus barbiger* | Brassicaceae | Herb | R |

*Note*: Status = rare (R), threatened (T), or endangered (E) according to CalFlora database (www.calflora.org).

range size and local abundance, Gaston (1994) proposed using the 25th percentile as a cut-off point to define rarity. However, because our pool of habitat specialists was so small, we used slightly broader definitions on the other two axes to obtain an adequate number of triply rare species for robust statistical analyses. Of the 939 species, we classified 341 species with range sizes $< 41{,}269$ km$^2$ as small-range species. We classified the 279 herbs with mean cover values $< 0.1\%$, and the 79 trees and shrubs with local cover values $< 1.0\%$, as locally sparse species. These cut-off points corresponded to the lowest 36th percentile of range sizes, and the lowest 38th percentile of local cover values for each life form considered separately. There were 29 triply rare species in 15 families under these definitions, of which 25 were herbs and 4 were shrubs; 16 are currently considered rare, 1 threatened, and 1 endangered in the California Native Plant Society inventory of rare species (Tables 1 and 2).

## Environmental, intrinsic, and evolutionary data

Environmental traits for all 939 species were obtained by intersecting species ranges (Viers *et al.* 2006) with a California state climate model (Daly *et al.* 1994) and a state geologic map (Jennings 1977). Climate for each species was measured by taking a spatial average over its geographic range for the 30-year mean of annual rainfall, July rainfall, maximum July temperature, and minimum January temperature. To measure habitat availability for each species, we needed an indicator that was not biased either by range size (e.g., the total area of serpentine within the species range would be systematically larger for species with larger ranges) or by the degree of habitat specialism (e.g., the percentage of the species range that is serpentine would by definition always be 100% for habitat specialists). The total area of serpentine within a fixed radius of the species' range center meets these two criteria. For each species, we computed the amount of serpentine within radii of 10 km and 100 km of the centroid of the species' range (314 km$^2$ and 31,415 km$^2$, respectively). These values were corrected for the percentage of these circles that did not overlap with land area.

Life form (herbaceous vs. woody) and life history (annual vs. perennial) were the only intrinsic traits with clear relevance to extinction risk for which data were available for all 939 of our study species. We note that Hegde & Ellstrand (1999) compared the traits of Californian rare, threatened, or endangered species (Skinner & Pavlik 1994) with a group of species described as abundant or common by the state flora (Hickman 1993), and found the rare species to have higher woodiness, lower monocarpy, shorter stature, more many-seeded and/or dehiscent fruits, and lower maximum elevations than common species. However, the rare, threatened, and endangered list (Skinner & Pavlik 1994) includes many anthropogenically rare species, whereas our hypothesis that rare species should be found in favorable environments applies only to rarity that is primarily natural.

To categorize species in terms of evolutionary history, we used the biogeographic interpretation of the Californian flora by Raven & Axelrod (1978). We considered 424 species to belong to rapidly speciating groups, based on their membership in one of the 55 genera

**Table 2** Numbers of species found in each of the rarity/commonness categories

| Range | Large | | Small | |
|---|---|---|---|---|
| Specialism: | Broad | Narrow | Broad | Narrow |
| Cover: sparse | 207 | 0 | 122 | 29 |
| Not sparse | 387 | 2 | 148 | 42 |

or 14 higher taxa that these authors classified as California Floristic Province endemics, or one of the 45 genera of north-temperate affinity that they considered to have undergone extensive diversification within the Province. These groups are believed to have speciated rapidly in the 1–2 million years since the onset of the Mediterranean-type climate, and are characterized by large numbers of species that are often shallowly differentiated from one another (Stebbins & Major 1965; Raven & Axelrod 1978). Other groups in the California flora are considered by these sources to have undergone most of their major diversification prior to the modern climate.

## Analyses

Contingency table analyses were used to test for nonrandom associations among the three forms of rarity, and to test for associations between triple rarity and life history traits (intrinsic-trait hypothesis) and triple rarity and membership in recently diversifying taxa (rapid-speciation hypothesis).

Discriminant analysis was used to determine which combinations of climatic conditions and habitat availability best predicted triply rare status for individual species. To accomplish this, we first used PROC STEPDISC in SAS Institute (2003) SAS 9.1 to select sets of variables and interaction terms capable of distinguishing groups. PROC DISCRIM was then performed using the variables selected using the stepwise procedure. Finally, mean differences in climatic and habitat associations for triply rare versus other species were compared to describe the differences between groups in habitat associations. For mean comparisons, Bayesian techniques were used and Markov chain Monte Carlo procedures implemented in WinBUGS (Spiegelhalter *et al.* 2002) to permit "exact" estimates of posterior distributions and credible intervals. To facilitate a comparison of the results to conventional frequentist means comparisons, posterior probabilities were calculated for the hypothesis that mean differences differ from the null hypothesis of 0.0 (Woodworth 2004). All these analyses were repeated comparing triply rare species with only their congeners to control for taxonomic bias (Kunin & Gaston 1993; Murray *et al.* 2002; Kelly & Woodward 2005).

## Results

Contingency table analyses showed that small-range rarity was positively associated with habitat specialism (Pearson $\lambda^2 = 825.6$, 1 *df*, $P < 0.001$), and also positively associated with local sparsity (Pearson $\lambda^2 = 8.4$, 1 *df*, $P = 0.004$). There was some evidence that habitat specialism was negatively associated with local sparsity (Pearson $\lambda^2 = 0.78$, 1 *df*, $P = 0.08$).

Stepwise discriminant analysis for triply rare versus other species revealed an interactive relationship between habitat and climate, such that whenever sufficient surrounding habitat (within 10 km of the plot) was present, benign climatic conditions further distinguished the situations in which rare species were found. Using the conventional probability of entry into the model of $P < 0.15$, all interactions between habitat availability and climatic conditions were included (Table 3). Discriminant ability, as indicated by the canonical correlation of the discriminant function with rarity status, was 0.42. The last variable entered—the interaction with July precipitation minimum—contributed little to the canonical correlation. Posterior means and credible intervals for climatic and habitat differences between triply rare and other species are given in Table 4, along with probabilities for the hypothesis that observed group differences are nonzero. Triply rare species were, on average, found in areas with higher mean annual precipitation, higher July minimum precipitation, lower July maximum temperature, higher July minimum temperature, higher January minimum temperature, and greater amount of their specialized habitat type within 10 km. Posterior probabilities for differences between groups were generally high ($\geq 0.90$).

Similar findings were obtained when the 29 triply rare species were compared only with their 131 congeners. The primary difference was that only two interactions, habitat with January minimum temperature and habitat with mean annual precipitation, contributed to the discriminant function (Table 5). Despite the simpler

**Table 3** Stepwise discriminant analysis results for triply rare versus nonrare species. Prediction accuracy was estimated at 92%

| Variable(s) | *F*-value | $P > F$ | Wilk's λ | $P > \lambda$ | Canonical Correlation | $P >$ ascc |
|---|---|---|---|---|---|---|
| All climate variables | 20.61 | < 0.0001 | 0.900 | < 0.0001 | 0.32 | < 0.0001 |
| Habitat ∗ Jan. temp. min. | 60.73 | < 0.0001 | 0.844 | < 0.0001 | 0.39 | < 0.0001 |
| Habitat ∗ mean ann. precip. | 17.51 | < 0.0001 | 0.829 | < 0.0001 | 0.41 | < 0.0001 |
| Habitat ∗ Jul. temp. max. | 5.16 | 0.0234 | 0.824 | < 0.0001 | 0.42 | < 0.0001 |
| Habitat ∗ July precip. min. | 3.02 | 0.0826 | 0.8214 | < 0.0001 | 0.42 | < 0.0001 |

**Table 4** Mean differences between triply rare and other species in climatic and habitat conditions

| Variable | Group | *Lower* | *Mean* | *Upper* | *Difference* | *Posterior probability* |
|---|---|---|---|---|---|---|
| Mean annual precipitation | Nonrare | 83.8 | 85.7 | 87.7 | | |
| | Rare | 82.1 | 98.9 | 115.7 | 13.2 | 0.90 |
| July precip. minimum | Nonrare | 0.0104 | 0.014 | 0.0176 | | |
| | Rare | 0.0243 | 0.073 | 0.122 | 0.0586 | 0.98 |
| July temp. maximum | Nonrare | 38.6 | 38.8 | 39.0 | | |
| | Rare | 34.6 | 35.3 | 36.0 | −3.50 | ∼ 1 |
| Jan. temp. minimum | Nonrare | −12.5 | −12.1 | −11.7 | | |
| | Rare | −4.7 | −3.35 | −2.00 | 8.75 | ∼ 1 |
| Habitat w/in 10-km buffer | Nonrare | 0.650 | 0.733 | 0.817 | | |
| | Rare | 1.924 | 2.49 | 3.04 | 1.76 | ∼ 1 |

Note: Results are based on predictive posterior distributions for parameters. Presented are the lower 95% CI, mean, upper 95% CI, differences between means for triply rare versus other species, and the posterior probabilities that the mean differences deviate from zero by > 1.96 standard errors.

model, discriminant ability was greater for the congener-only comparison (0.56) than for the comparison to all species (0.42). Posterior means and credible intervals for climatic and habitat differences between triply rare and other congeners are given in Table 6. Triply rare species compared with their congeners were, on average, found in areas with higher mean annual precipitation, with a higher July minimum precipitation, with a lower July maximum temperature, with a higher July minimum temperature, with a higher January minimum temperature, and with a greater amount of their specialized habitat type within 10 km. Posterior probabilities for differences between groups were high for July temperatures, January temperatures, and habitat availability. For July precipitation minimum, we estimate a 84% probability for the difference being greater than zero whereas for mean annual precipitation, we estimate only a 62% probability. Conventional error rates of 5% chance of a type I error would suggest that these last two differences between groups are not of high reliability.

Considering the three individual axes of rarity, the small-range species and habitat-specialist species inhabited more benign environments than large-range and nonspecialist species, respectively, with each model identifying higher habitat availability plus a slightly different set of climatic variables; however, locally sparse species did not differ in their environmental affinities from nonsparse species (results not shown). Triply rare species did not differ from all other species in their frequencies of herbaceous and woody species (Pearson $\chi^2 = 0.06$, 1 *df*, $P = 0.81$) or of annual and perennial species (Pearson $\chi^2 = 1.2$, 1 *df*, $P = 0.28$). Rare and nonrare species on each of the three individual axes also did not differ in these respects.

Triply rare species had a slightly higher tendency to belong to higher taxa considered to have undergone rapid recent speciation, but this difference was not supported statistically (55% of triply rare species vs. 45% of all species; Pearson $\chi^2 = 1.2$, 1 *df*, $P = 0.28$). However, this difference was supported for small-range species (53% of small-range species; Pearson $\chi^2 = 14.3$, 1 *df*, $P < 0.001$) and habitat specialists (56% of habitat specialists; Pearson $\chi^2 = 3.8$, 1 *df*, $P = 0.05$).

## Discussion

Favorable environmental conditions emerged in this study as predictive characteristics of rare species, those that had small ranges, specialized habitats, and low local abundances. Such species were found within regions that contained larger areas of their specialized habitat, as

**Table 5** Stepwise discriminant analysis results for triply rare versus nonrare congeners. Prediction accuracy was estimated at 82%

| Variable(s) | *F*-value | $P > F$ | Wilk's λ | $P > \lambda$ | Canonical Correlation | $P >$ ascc |
|---|---|---|---|---|---|---|
| All climate variables | 10.02 | < 0.0001 | 0.754 | < 0.0001 | 0.50 | < 0.0001 |
| Habitat ∗ Jan. temp. min. | 10.25 | = 0.0017 | 0.707 | < 0.0001 | 0.54 | < 0.0001 |
| Habitat ∗ mean ann. precip. | 4.23 | = 0.041 | 0.688 | < 0.0001 | 0.56 | < 0.0001 |

**Table 6** Mean differences between triply rare and their nonrare congeners in climatic and habitat conditions

| Variable | Group | Lower | Mean | Upper | Difference | Posterior probability |
|---|---|---|---|---|---|---|
| Mean annual precipitation | Nonrare | 81.8 | 87.8 | 93.7 | | |
| | Rare | 82.0 | 98.8 | 115.4 | 11.0 | 0.62 |
| July precip. minimum | Nonrare | 0.0122 | 0.0255 | 0.0385 | | |
| | Rare | 0.0256 | 0.0731 | 0.121 | 0.0476 | 0.84 |
| July temp. maximum | Nonrare | 37.3 | 37.84 | 38.4 | | |
| | Rare | 34.6 | 35.31 | 36.0 | −2.53 | ∼ 1 |
| Jan. temp. minimum | Nonrare | −10.9 | −9.79 | −8.72 | | |
| | Rare | −4.71 | −3.35 | −1.99 | 6.44 | ∼ 1 |
| Habitat w/in 10-km buffer | Nonrare | 0.726 | 0.954 | 1.186 | | |
| | Rare | 1.93 | 2.49 | 3.05 | 1.54 | ∼ 1 |

*Note*: Results are based on predictive posterior distributions for parameters. Presented are the lower 95% CI, mean, upper 95% CI, differences between means for triply rare versus other species, and the posterior probabilities that the mean differences deviate from zero by $> 1.96$ standard errors.

compared with more common species sharing the same habitat. Subject to habitat availability, the distributions of triply rare species were characterized by higher total and summer rainfall, higher winter temperatures, and lower summer temperatures than those of more common species. Triply rare species differed in similar ways from their more common congeners, but the congener-only analysis showed a greater role for habitat availability and seasonal temperature extremes and less for rainfall as contrasted with the all-species analysis. This hierarchical comparison suggests that habitat availability and temperature extremes influence the geographic distributions of rare versus more common species within the genera that contain rarities, whereas rainfall primarily influences the distributions of the rarity-containing genera versus other genera. Because the rarest taxa in this flora are found in the more benign environments, it is clear that their comparative rarity is not the result of harsher environmental conditions, in contrast to some other rarity analyses in which the direction of cause and effect may be ambiguous (Gaston & Kunin 1997). These results are also not likely to reflect anthropogenic processes because environmental conditions associated with rare species in our study are different than those that predict the severity of human impacts on biodiversity in California (Seabloom *et al.* 2002, 2006; Schwartz *et al.* 2006). Large areas of serpentine, moderate temperatures, and medium to high rainfall are found in sparsely populated north-western California, whereas human impacts are concentrated in the southern and central coastal regions (Seabloom *et al.* 2002, 2006).

Our results are consistent with an interpretation based on natural rarity and climatic history. Like other biotas around the world, including (but not limited to) other Mediterranean-climate floras, the flora of California has been strongly shaped by a history of climatic oscillations interacting with a geologically and topographically complex landscape (Cowling *et al.* 1996; Calsbeek *et al.* 2003; Thompson *et al.* 2005). Relictual and fossil taxa characteristic of mesic environments found within presently arid regions testify to the many regional and global extinctions that have been caused by past episodes of climate change (Raven & Axelrod 1978; Edwards 2004). Given this background, it is to be expected that narrowly distributed habitat-specialist taxa are not now evenly distributed throughout the State's highly variable climates. Instead, they tend to be found in areas where they are sheltered from the extremes of heat, cold, and drought, and in regions where their special habitat (in this case, serpentine soil) is spatially extensive. This interpretation is broadly consistent with the hypothesis of Jansson & Dynesius (2002), who proposed that climatic stability is associated with the persistence of specialized species, whereas climatic instability is associated with lower habitat specialization as well as overall lower species diversity. Our findings highlight that high levels of rarity, endemism, and overall species richness may be expected to occur in regions that provide conditions that allow rare habitat specialists to resist climatically driven extinctions (Jansson & Dynesius 2002; Jetz *et al.* 2004).

Edaphically restricted plants are emblematic of species that may be poorly equipped to cope with rapid future climate change because of their often sparse and widely scattered habitat. Climate models for California agree that temperatures will increase, but changes in the amount, timing, and spatial distribution of precipitation are as yet uncertain, with predictions for the overall change ranging from a 50% decrease to a 200% increase (Hayhoe *et al.* 2004). Serpentine soils are found predominantly in three ecological regions of the state: the northwest, including the northern coastal range and the Klamath

Mountains; the central coastal range, from the San Francisco Bay Area south; and the foothills of the Sierra Nevada mountains to the east. The northwestern region has the coolest summer temperatures, highest rainfall, and the largest areas of serpentine, and the large serpentine outcrops in this region are topographically heterogeneous, facilitating natural shifts to compensate for climatic changes (e.g., Thuiller *et al.* 2006a). In this region, we suggest that rare serpentine plants are likely to persist without active intervention as long as existing natural habitats remain unfragmented; fortuitously, much of this region is in public ownership. In contrast, the serpentine outcrops of the central coast and Sierran foothills are smaller, occur in warmer and drier climates, and are relatively uniform topographically. In these regions, which are also under heavier development pressure, our results suggest that active measures such as ex situ conservation or assisted migration (McLachlan *et al*. 2007) may be critical for the preservation of rare serpentine plants.

Dominant themes in contemporary conservation practice include "managing landscapes in the face of uncertainty" (Burgman *et al.* 2007) and "managing for adaptive change when it may no longer be appropriate to use historical conditions as the target" (Seastedt *et al.* 2008). Our case study of rare serpentine plants in California illustrates these themes. Even though we lack full information on future climates, our analysis allows us to evaluate the heightened importance of climate for rare species, to partition the flora we studied into geographic regions where rare species face greater or lesser risks, and to anticipate the relative utility of multispecies refugia versus active species-by-species management. The next steps would include conducting detailed risk assessments and creating appropriate strategies for each at-risk rare species, and identifying the key geographic areas that may serve as refugia and corridors for multiple species using niche-based modeling of species, functional groups, and vegetation types (e.g., Williams *et al.* 2005; Thuiller *et al.* 2006a, b; Hannah *et al.* 2007). Such an exercise should be considerably improved by the next generation of regionally detailed climate projection models for the state, that are not yet available.

Other studies have examined the comparative risks faced by the different components of particular floras or faunas; they have yet to reach a consensus as to whether endemic species are at greater or lesser risk than nonendemics, and some studies suggest that the answer depends on the climatic and life-form traits of the particular species (Thuiller *et al.* 2006b). However, we are unaware of any previous studies that have considered all three rarity axes when comparing the climatic sensitivities of rare versus nonrare species within any given biota. We believe that our hypothesis associating such species with heightened sensitivity to environmental favorability has the potential for broad applicability to other biotas. Especially promising places to test further this idea would be the other Mediterranean climate zones of the world, since all are exceptionally rich in geographically restricted plant species, and most include large numbers of edaphic endemics as well as high levels of rarity (Cowling *et al.* 1996). Within these regions, the highest levels of plant diversity are generally associated with high rainfall, topographic heterogeneity, and/or edaphic complexity (Cowling *et al.* 1996), all of which suggests the potential for strong parallels with the system we studied. However, in principle, the favorable-environment hypothesis could apply equally well to animals, non-Mediterranean climates, and niche specialization that is unrelated to soils.

We conclude that in the flora we studied, spatially extensive habitats and benign climates have helped rare species persist in the past and can be expected to have a heightened influence on their future survival. It is increasingly recognized that effective conservation planning requires understanding the dynamic processes underlying species distributions (e.g., Medail & Quezel 1999; Midgley *et al.* 2002; Cowling *et al.* 2003; Williams *et al.* 2005; Thuiller *et al.* 2006a; Thuiller *et al.* 2006b; Hannah *et al.* 2007; McLachlan *et al*. 2007). As strategists begin to target critical habitats, conduits for dispersal, and modes of human intervention to conserve biodiversity in an era of rapid global change, we believe it is important to emphasize the particular environmental factors that have enabled the "rarest of the rare" to persist through millennia of changing environments.

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