

Characterizing habitat suitability for disturbance-dependent rare plants of gabbro soils

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Assessing habitat quality to identify the highest priority sites for conservation planning is a complex task, and requires an understanding of which habitat attributes are most important for species population success. I explored the relative importance of biotic, abiotic, spatial, or disturbance-related habitat attributes to the population abundance of four edaphic-endemic, disturbance-dependent rare plant species. Variable selection provided a way to evaluate the relative importance of ecologically relevant groups of habitat attributes. Overall, biotic and disturbance history variables were the best predictors of population abundance for all four gabbro rare plant species, while spatial and abiotic variables were not found to be strong drivers of population abundance. Habitat quality for the four rare plants evaluated here may be best characterized by the associated species in the vegetation community, and an appropriate disturbance regime is a key component to maintain populations over time.

Key words: rare plants, disturbance, edaphic endemic, AIC, model selection, gabbro

Understanding the habitat attributes that shape habitat suitability for species has been a continuing theme in ecological research for the past century (Grinnell 1914, 1917; Kruckeberg 1954; Hutchinson 1959; Hirzel and Lelay 2008), and is an essential step in identifying high priority sites for conservation planning (Prendergast et al. 1999). Assessing habitat quality is a complex task that requires an analysis of the relationship between species distributions, population viability, and habitat conditions (Johnson 2007). New statistical methods allow for analyses of large datasets with many variables, which can for the first time begin to untangle the complex relationships between suites of habitat attributes and habitat quality (e.g., Schlesinger et al. 2008).

Determining the components of habitat quality for disturbance-dependent plants, such as species adapted to fire-driven systems, poses a special challenge because these species rely on transient habitat types (e.g., early-successional) and habitat quality varies during succession. Sites important for long-term conservation may fail to be identified because they appear unoccupied even though the species is actually present in the seedbank. The conservation of currently occupied sites may not guarantee successful conservation of the species over long time periods if the site loses required habitat qualities (Drechsler et al. 2009). A matrix of suitable habitats at different successional stages may be necessary for conservation; however, identifying suitable but unoccupied habitat is challenging (Quintana-Ascencio 1998). The distributions of early-successional species appear to be driven largely by random disturbance events such as fire (Vuilleumier et al. 2007); however, abiotic, biotic, and spatial factors also play a role in shaping the distributions of disturbance-dependent rare plants (Maliakal-Witt et al. 2005, Moretti et al. 2008).

Habitat quality has been measured for plants in a number of ways including (1) biotic community composition (e.g., Munzbergova 2004); (2) site history (e.g., Ross et al. 2002, Evans et al. 2008); (3) physical environmental gradients (e.g., Whittaker 1960, Woodward and Williams 1987); and (4) habitat spatial configuration (e.g., Wolf and Harrison 2001, Boyle et al. 2002). Four main ecological and conservation paradigms provide frameworks for assessing habitat quality based on vegetation classification, site history and succession, ecological niches, and patch dynamics. These frameworks are not mutually exclusive, and more than one may have explanatory power for predicting the distribution and abundance of species in a system.

Vegetation classification categorizes habitats based on dominant or indicator plant species (Sawyer et al. 2009). The use of vegetation classification in conservation emphasizes the importance of biotic habitat attributes, including community composition and associated species, as measures of habitat suitability. Vegetation type is commonly used to predict species presence in wildlife-habitat relationships programs (Morrison et al. 1998), and has recently been applied in large conservation planning efforts in which vegetation type is used as a surrogate to capture plant and animal biodiversity across the landscape (e.g., Reyers et al. 2007). Biotic community attributes such as associated species (Munzbergova 2004, Elmendorf and Moore 2008) have been shown to predict plant species presence, abundance, and reproductive output.

Site history represents a process-based conservation paradigm that emphasizes the roles of disturbance, restoration, and the maintenance of successional processes for habitat suitability (Pickett et al. 2009). Site history and disturbance have been identified as key components of species occupancy patterns in fragmented landscapes (Bastin and Thomas 1999, Ross et al. 2002). Furthermore, local-scale disturbance, such as edge effects, can explain species distribution and abundance better than habitat or community models in some systems (Harrison 1997, Benitez-Malvido 1998). Evans et al. (2008) showed that time since last fire can have a direct effect on the demography of disturbance-dependent plants; therefore, management to ensure proper disturbance regimes may be an essential component of a conservation strategy for such species.

The niche modeling paradigm predicts that physical environmental gradients define the habitat areas in the landscape where a species has the potential to occur (potential niche), and biotic interactions further limit the habitat in which the species actually occurs (realized niche: Grinnell 1914, 1917; Hutchinson 1959). Numerous studies have found that physical gradients, including climate, topography, and soils, are strong predictors of plant distributions

(Whittaker 1960, Kruckeberg 1984, Woodward and Williams 1987, Wolf and Harrison 2001). A large body of recent work has focused on the use of ecological niche modeling to understand species distributions and inform conservation (Elith and Leathwick 2009).

The patch dynamic paradigm, shown in metapopulation (Levins 1969, Moilanen and Hanski 1998) and mainland-island (MacArthur and Wilson 1967) models, predicts population presence and persistence based on the spatial configuration of habitat. Conservation actions based on this framework emphasize the role of large, connected areas to maintain habitat quality and allow population persistence over time. However, studies have shown that small, isolated preserves may be valuable for conserving species with narrow distributions, particularly if there is little remaining habitat (Lesica and Allendorf 1992, Shafer 1995), and small, isolated patches of rare plants may persist well over time in small preserves (Lawson et al. 2008). Despite that, reproductive output in small or fragmented plant populations may be reduced, even in species that naturally occur in small, patchy populations (Groom 2001, Wolf and Harrison 2001). Furthermore, small reserves may suffer from area-related changes in habitat quality (Hokit and Branch 2003). Early-successional species that rely on fire to maintain their populations may be particularly sensitive to habitat fragmentation if it results in changes to the fire return interval (Leach and Givnish 1996).

This study was conducted in an area of gabbroic soils surrounding Pine Hill in El Dorado County, California. The Pine Hill Preserve system was established in 2001 to conserve rare-plant habitat in this region, and there is currently an effort underway to identify habitat for addition to the preserve system (USFWS 2002). Land prices in this area can vary substantially depending on location, compounding the need for a tool to assess relative conservation value (i.e., habitat quality) of different sites to set conservation priorities for the best allocation of limited conservation funds. Because the focus of conservation actions often differs depending on which paradigm lens (vegetation classification, site history and succession, ecological niches, or patch dynamics) is used to view the system, exploring the relative contribution of each framework to explain observed species distributions may help identify the best conservation and management approach for a species.

METHODS

Study system.—This study was conducted within a 104-km² area of mafic, gabbroic soils surrounding Pine Hill in western El Dorado County, California (hereinafter referred to as the PHC), which is bisected on the southern end by US Hwy 50, and is fragmented by residential development. Gabbroic soils are considered intermediate to serpentine and metamorphic rock, and sometimes support unique plant communities (Alexander 1991). The PHC has a high botanical diversity, including eight rare plants, four of which are gabbro endemics. This study focused on four of the PHC rare plant species that occur primarily in chaparral openings and rely on fire or other disturbances to maintain populations over time: two gabbro endemics, *Wyethia reticulata* Greene (Asteraceae) and *Ceanothus roderickii* W. Knight (Rhamnaceae), and two species endemic to gabbro and serpentine substrates in the Sierra Nevada foothills, *Calystegia stebbinsii* Brummit (Convolvulaceae) and *Packeria layneae* (Greene) W.A. Weber & A. Love (Asteraceae). Although they all co-occur within the same habitats, these four species have slightly different distributions, life history characters, and mechanisms for persisting through successional cycles (Table 1).

TABLE 1.—Life-history characters of the four gabbro rare plants at Pine Hill, California. Rarity status is abbreviated as follows: FE=federally listed endangered; FT=federally listed threatened; SE=state-listed endangered; SR=state-listed rare; BLM-S=Bureau of Land Management sensitive.

Species	Common name	Family	Rarity status	Known substrates ^a	Counties of occurrence ^a	Dispersal mechanism	Life-form	Response to fire	Vegetative persistence during inter-fire period	Seed-bank
<i>Calystegia stebbinsii</i>	Stebbins' morning-glory	Convolvulaceae	FE, SE	gabbro, serpentine	El Dorado, Nevada	gravity ^b	perennial herb	increased germination ^{c,f}	no	yes ^{e,t}
<i>Ceanothus roderickii</i>	Pine Hill ceanothus	Rhamnaceae	FE, SR	gabbro	El Dorado	gravity	shrub	increased germination ^{f,g}	limited	yes ^{f,g}
<i>Packera layneae</i>	Layne's ragwort	Asteraceae	FT, SR	gabbro, serpentine, metamorphic	El Dorado, Tuolumne, Yuba, Butte, Placer	wind	perennial herb, clonal ^c	resprouts ^h	yes	no ^h
<i>Wyethia reticulata</i>	El Dorado County mule ears	Asteraceae	BLM-S	gabbro	El Dorado	gravity	perennial herb, clonal ^d	resprouts, increased flowering ^{d,g}	yes	no ^f

^aCalifornia Natural Diversity Database (2014)

^bAnts have also been observed carrying the seed (M. Gogol-Prokurat, personal observation), although their role as a dispersal agent is unknown

^cD. Ayres, UC Davis, and L. Fety, Bureau of Land Management, unpublished data

^dAyres and Ryan (1997)

^eNosal (1997)

^fAyres (2011)

^gBoyd (1987)

^hD. Ayres and L. Fety, personal observation

Sampling strategy.—Plot locations were randomly stratified across chaparral and oak woodland vegetation types on public lands using ArcGIS and aerial photographs. Because it was not possible to achieve 30 presence plots for each of the rare plants using random sampling, additional plots were haphazardly stratified across rare plant patches observed in the field. All rare plant plots were separated by >100 m. Relevé data on environmental conditions representing biotic community composition, abiotic attributes, spatial configuration, and disturbance history (Table 2), as well as rare plant presence and population size were collected at each location in nested 10 m² and 400 m² plots during 2005, 2006, and 2007.

Abiotic variables included topographic position, soil color and texture, and coarse fragments (rock and litter layer). Topographic position was measured using a standard compass. Although mineral content has been shown to influence rare plant presence and abundance on serpentine soils (Kruckeberg 1954, Wolf and Harrison 2001), a recent study of the mineral content of gabbro soils found no significant differences in chemical composition between sites that were occupied and unoccupied by rare plants in the PHC (Alexander 2011). I chose simple measures of soil properties that are easy to implement in the field, including color, texture, and rockiness. Soil color (i.e., redness) represents properties such as Fe content (Schwertman 1993), and was measured using Munsell's (2000) color chart. Soil texture was measured using a simplified key to soil types adapted from Brewer and McCann (1982), which was converted to an ordinal scale representing clay content. The percent cover of coarse fragments of various types (litter, boulders and bedrock, stones, and gravel) was estimated in each plot.

I collected a full species list of plants present in the 10 m² plot to capture microhabitat conditions directly surrounding the rare plant occurrences, and a list of the dominant species within each layer (tree, shrub, herb) in the 400 m² plot to characterize the larger vegetation community in which the rare plants occurred. Each plot was visited at least once early in the season (March–May) and once late-season (June–August) to ensure a full species list.

TABLE 2.—Explanatory variables used in multiple linear regression models for *Calystegia stebbinsii* (CAST), *Ceanothus roderickii* (CERO), *Packera layneae* (PALA), and *Wyethia reticulata* (WYRE), Pine Hill, California.

	Variable	Description	
Spatial Factors	Connectivity metric	CAST and PALA connectivity = (Σ area/distance of all patches of plants within 300 m of a plot) CERO and WYRE connectivity = (1/distance to nearest patch)	
	Location	UTMN UTM Northing, NAD83 UTME UTM Easting, NAD83	
	Habitat area	Vegetation patch area Alliance-level vegetation patch, minimum mapping unit 0.4-0.8 ha Local patch area vegetation patch, minimum mapping unit <0.4-0.8 ha, patches separated by anthropogenic linear features such as roads	
Biotic Factors	Vegetation community composition	PCA1 PCA2 PCA3 PCA axes of arcsine-square root transformed cover values of the dominant species present in the 400-m ² plots. Chaparral shrubland was associated with PCA1 in a positive direction, while sites characterized by species indicating recent fire were associated with PCA1 in a negative direction. Xeric chaparral and grassland habitats were associated with PCA2 in a positive direction, while mesic woodland was associated with PCA2 in a negative direction. Chaparral shrubland was associated with PCA3 in a positive direction, and mesic chaparral and woodland species were associated with PCA3 in a negative direction.	
		Nat. Rich. Native richness = # native species in 10-m ² plot	
		Non-native cover Percent non-native cover = total non-native cover / total vegetation cover	
		Epiph. lichen Presence of epiphytic lichen	
	Vegetation structure	Tall Cover % tall cover (>4 m) in 10-m ² plot Medium cover % medium cover (0.5-4 m) in 10-m ² plot Low cover % low cover (<0.5 m) in 10-m ² plot	
	Abiotic Factors	Topography	Elevation Elevation (feet) Slope Slope (degrees) Aspect Northness = cosine (aspect in radians)
Soil properties		Soil Redness measured using Munsell's color chart Clay content Ranking of clay content based on simplified key to soil types adapted from Brewer and McCann (1982)	
Coarse fragments		Litter % litter cover in 10-m ² plot Boulder and Bedrock % boulder (>60 cm diameter) and bedrock cover in 10-m ² plot Stoniness % cover stones (7.5-60 cm) in 10-m ² plot Gravel % cover gravel (2 mm-7.5 cm) in 10-m ² plot	
Disturbance		Edge effects	Distance to edge distance between the plot and the nearest paved road or developed area >0.4 ha
		Site history	Clearing presence of grading or clearing noted in plot Fire presence of recent fire noted in plot
		Successional status	regeneration % of total shrubs regenerating (<3 years old) senescence % of total shrubs present with >25% dead branches

The abundance (number of individuals within the 400 m² plot) of each rare plant was counted in each plot. If there were >1000 individuals present, abundance was estimated by counting the number of individuals in a subplot and multiplying by occupied area. Plot locations were recorded and the perimeter of the rare plant patches sampled were field mapped using a Garmin 12XL GPS unit (accurate to <4 m). Additional rare plant patches throughout the PHC were field mapped for the development of connectivity metrics. For data analysis, abundance within 400 m² was chosen as the primary measure of population size because it represents an intermediate between total number of individuals per population, density of individuals (plants/m²), and total patch area (m²) that is standardized and easily repeatable.

Data analysis.—I used an Akaike's Information Criteria (AIC) model selection approach to determine which spatial, biotic, abiotic, and disturbance history variables best predicted population abundance of each of the four rare plant species using multiple linear regression. AIC allows for selection of the most parsimonious models based on goodness-of-fit (r^2) by including a penalty for model complexity (number of variables) to discourage model overfitting. I first tested for correlations among explanatory variables to ensure that none were highly collinear (Pearson's $r > 0.7$). Model selection was a two-step process: (1) identifying core variables with the greatest explanatory power by assessing models with all possible combinations of variables within each core group, and (2) building final models based on the selected core variables. For each species, the best final models with $\Delta\text{AIC} \leq 2$ were selected. In all cases, the AICc, which includes a correction for small sample sizes was used (Burnham and Anderson 2002). All analyses were run using *Statistica* 6 (StatSoft, Inc. 2003).

Plots were classified post-sampling according to the vegetation types identified by Wilson et al. (2009), which described four main vegetation types within the PHC: grassland, xeric chaparral, mesic chaparral, and oak woodland. Woodland plots were dominated by oaks (primarily *Quercus wislizeni* or *Q. kelloggii*) or by foothill pine (*Pinus sabiniana*). The two chaparral types were generally dominated by white-leaf manzanita (*Arctostaphylos viscida*) or chamise (*Adenostoma fasciculatum*), and were differentiated by the prevalence of four mesic indicator species: Brainerd's sedge (*Carex brainerdii*), redbud (*Cercis occidentalis*), toyon (*Heteromeles arbutifolia*), and hoary coffeeberry (*Frangula californica* ssp. *tomentella*). Vegetation stands including those species with cumulative cover values of >3% were classified as mesic chaparral, while stands in which those species were absent, or present with a cumulative cover value of <3%, were classified as xeric chaparral. Grassland plots were those with <10% cover trees or shrubs.

RESULTS

Overall, biotic and disturbance history variables had the strongest explanatory power for predicting population abundance for all species (Table 3). Biotic variables, including vegetation community composition and vegetation structure, were the strongest predictors of abundance for all species except *P. layneae*, for which disturbance history was the best predictor. Percent cover of gravel was the only abiotic variable that was a predictor of abundance for three of the four species. Spatial and abiotic variables identified as core variables during the first model selection step generally added little to model explanatory power based on AIC model selection, and were sometimes excluded from the final models (Table 3). Variables excluded from all models using AIC model selection included connectivity, local patch area, native richness, elevation, slope, aspect, percent cover litter, boulder and bedrock, and percent shrub regeneration.

TABLE 3.—Univariate contribution of core variables to predict population abundance in linear regression models for *Calystegia stebbinsii* (CAST), *Ceanothus roderickii* (CERO), *Packera layneae* (PALA), and *Wyethia reticulata* (WYRE), Pine Hill, California. Values for variables that were not identified as core variables are blank. Core variables included in all final models determined by AIC model selection are shown in bold. Core variables excluded from final models when all variables were considered are italicized.

Variable			Proportion of variance explained (r^2)			
			CAST	CERO	PALA	WYRE
Spatial Factors	Connectivity metric	<i>CAST and PALA</i> <i>CERO and WYRE</i>				
	Location	UTMN		0.28	0.04	
	Habitat area	UTME Vegetation patch area <i>Local patch area</i>	<0.01		0.01 0.15	0.12
Biotic Factors	Vegetation community composition	PCA1 PCA2 PCA3	0.16	0.3	0.04 0.13	
		<i>Nat. Rich.</i> Non-native cover		0.01		
		Epiph. lichen	0.18			
	Vegetation structure	Tall Cover Medium cover Low cover	0.03			0.19 0.28
	Topography	<i>Elevation</i> <i>Slope</i> Aspect		0.13	0.05	
	Soil properties	Soil Redness Clay content			<0.01 0.02	0.11 0.14
Abiotic Factors	Coarse fragments	<i>Litter</i> <i>Boulder and Bedrock</i> Stoniness Gravel				0.01 0.1 0.1
	Edge effects	Distance to edge		0.19	0.39	
	Site history	Clearing Fire	0.15			0.29
Successional status	<i>regeneration</i> <i>senescence</i>			0.23		

C. stebbinsii.—Models including vegetation community (PCA1), tall cover, epiphytic lichen presence, and recent fire best predicted *C. stebbinsii* population abundance. Abiotic and spatial core variables were excluded from all final models using AIC.

C. roderickii.—Models including vegetation community (PCA1), percent non-native cover, and shrub decadence best predicted *C. roderickii* abundance. Distance to edge and location (UTMN) were also included in some final models, but did not significantly improve model fit ($\Delta r^2 < 0.02$).

P. layneae.—Distance to edge was the dominant predictor of *P. layneae* abundance ($r^2 = 0.39$), and gravel cover and vegetation community (PCA1 and PCA2) further improved model fit ($0.05 \leq \Delta r^2 \leq 0.14$). Clay content, location (UTMN), and aspect were also included in some final models but did not significantly improve model fit ($\Delta r^2 \leq 0.02$).

W. reticulata.—Low vegetation cover, medium vegetation cover, soil redness, and stoniness were included in all final models. The inclusion of gravel cover, vegetation patch area, and clearing improved model fit somewhat ($\Delta r^2 \leq 0.05$).

Grouping plots into the Wilson et al. (2009) vegetation types based on indicator species further showed that vegetation community was a predictor of species presence for all species (Figure 1). The majority of *C. stebbinsii* and *C. roderickii* plots were found in xeric chaparral. Other species closely associated with xeric chaparral included *Eriodictyon californicum*, *Eriophyllum lanatum*, *Helianthemum* sp., and *Allium* sp. (Table 4). *P. layneae* and *W. reticulata* were more closely associated with mesic chaparral, which included associated species *Cercis occidentalis*, *Rhamnus ilicifolia*, *Frangula californica* ssp. *tomentella*, *Polygala cornuta*, and *Galium porrigens* (Table 4). *W. reticulata* was also associated with woodland, and was the only of the rare species closely associated with *Calochortus albus*, *Quercus wislizeni*, *Heteromeles arbutifolia*, *Toxicodendron diversilobum*, and *Lepechinia calycina* (Table 4).

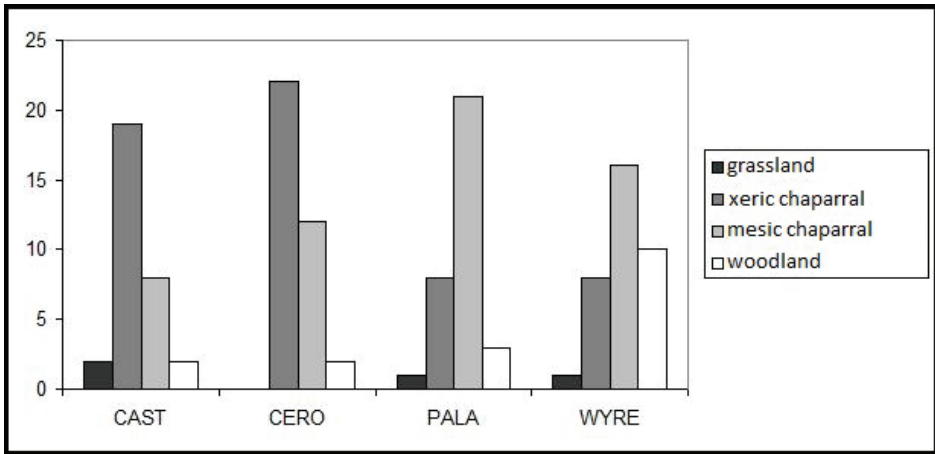


FIGURE 1.—Number of rare plant plots for *Calystegia stebbinsii* (CAST), *Ceanothus roderickii* (CERO), *Packera layneae* (PALA), and *Wyethia reticulata* (WYRE) assigned to the Wilson et al. (2009) Pine Hill, California gabbro vegetation types: grassland, xeric chaparral, mesic chaparral, and woodland.

TABLE 4.—List of species most frequently observed co-occurring with *Calystegia stebbinsii* (CAST), *Ceanothus roderickii* (CERO), *Packera layneae* (PALA), or *Wyethia reticulata* (WYRE) within 10-m² plots, Pine Hill, California. The 30 species most frequently associated with each rare species are in bold font. Incidence (Inc) is the percentage of plots occupied by each rare plant in which the associated species also was present. Cover (Cov) is the average percent cover of the associated species within those plots.

Scientific Name	CAST		CERO		PALA		WYRE	
	Inc	Cov	Inc	Cov	Inc	Cov	Inc	Cov
<i>Acmispon americanus</i>	29%	<1	42%	<1	24%	<1	23%	<1
<i>Adenostoma fasciculatum</i>	61%	2	67%	3	55%	6	83%	8
<i>Aira caryophylla</i>	77%	<1	88%	<1	83%	<1	87%	<1
<i>Allium</i> sp. ^a	39%	<1	39%	<1	17%	<1	10%	<1
<i>Anagallis arvensis</i>	29%	<1	42%	<1	41%	<1	33%	<1
<i>Arctostaphylos viscida</i>	61%	3	67%	4	83%	6	83%	6
<i>Brachypodium distachyon</i>	87%	2	94%	2	76%	1	57%	1
<i>Bromus madritensis</i>	29%	<1	42%	<1	76%	<1	70%	<1
<i>Calochortus albus</i>	13%	<1	6%	<1	10%	<1	40%	<1
<i>Calystegia stebbinsii</i>	100%	1	61%	2	28%	1	17%	1
<i>Carex brainerdii</i>	32%	2	42%	2	41%	3	30%	1
<i>Ceanothus lemmonii</i>	29%	1	33%	2	45%	3	53%	4
<i>Ceanothus roderickii</i>	71%	5	100%	6	52%	5	30%	3
<i>Centaurium tenuiflorum</i>	23%	<1	21%	<1	17%	<1	3%	<1
<i>Cercis occidentalis</i>	19%	1	33%	2	59%	1	33%	2
<i>Chlorogalum grandiflorum</i>	68%	1	85%	1	72%	1	30%	1
<i>Elymus multisetus</i>	19%	1	30%	<1	41%	<1	10%	<1
<i>Eriodictyon californicum</i>	26%	1	21%	<1	28%	1	7%	<1
<i>Eriophyllum lanatum</i>	23%	<1	24%	<1	14%	<1	20%	<1
<i>Festuca myuros</i>	68%	1	76%	1	76%	2	63%	1
<i>Frangula californica</i> var. <i>tomentella</i>	10%	2	18%	1	41%	1	43%	2
<i>Galium porrigens</i>	35%	<1	33%	<1	83%	<1	97%	<1
<i>Galium</i> sp. ^b	58%	<1	58%	<1	69%	<1	60%	<1
<i>Gastroidium phleoides</i>	94%	<1	100%	<1	86%	<1	80%	<1
<i>Helianthemum</i> sp. ^c	45%	1	30%	<1	24%	<1	17%	<1
<i>Hemizonella minima</i>	19%	<1	30%	<1	31%	<1	43%	<1
<i>Hesperolinon micranthum</i>	68%	<1	76%	<1	69%	<1	53%	<1
<i>Heteromeles arbutifolia</i>	0%	0	12%	1	21%	1	50%	3
<i>Hypericum concinnum</i>	29%	<1	24%	<1	34%	<1	33%	<1
<i>Hypochoeris glabra</i>	39%	<1	42%	<1	52%	<1	27%	<1
<i>Leontodon saxitilis</i>	87%	<1	94%	1	86%	1	47%	1
<i>Lepechinia calycina</i>	6%	<1	24%	1	21%	1	37%	3
<i>Logfia gallica</i>	94%	<1	91%	<1	72%	<1	53%	<1
<i>Navarretia filicaulis</i>	16%	<1	27%	<1	31%	<1	30%	<1
<i>Pinus sabiniana</i>	23%	2	18%	2	34%	1	37%	6
<i>Polygala cornuta</i>	10%	1	21%	<1	38%	1	57%	1
<i>Quercus wislizeni</i>	13%	<1	15%	<1	28%	1	53%	7
<i>Rhamnus ilicifolia</i>	23%	1	36%	1	55%	1	80%	2
<i>Salvia sonomensis</i>	90%	3	100%	3	100%	6	83%	5
<i>Sanicula bipinnatifida</i>	74%	1	85%	<1	76%	<1	60%	<1
<i>Packera layneae</i>	26%	1	39%	1	100%	1	30%	1
<i>Toxicodendron</i> <i>diversilobum</i>	3%	<1	3%	<1	10%	2	50%	3
<i>Wyethia reticulata</i>	13%	6	24%	5	34%	2	100%	9

^a*Allium peninsulare* or *A. sanbornii*

^b*Galium murale*, *G. parisiense*, or *G. divaricatum*

^c*Helianthemum suffrutescens* or *H. scoparium*

DISCUSSION

Overall, biotic community composition and disturbance history were the strongest predictors of species population abundance for the four gabbro rare plant species, while spatial habitat configuration and abiotic environmental variables were less important. The method of variable selection used provided a way to evaluate the relative importance of ecologically relevant groups of habitat attributes in predicting population abundance, which may be useful in ranking habitat quality (Johnson 2007), as well as identifying possible management actions that could improve habitat quality.

Biotic community composition was a strong predictor of population presence or abundance for all four rare species, supporting the findings of Munzbergova (2004) and Elmendorf and Moore (2008), that species composition in the vegetation community can be used to predict habitat suitability for plant species. Classifying sites by vegetation community type using indicator species was also informative for predicting habitat suitability. The dominant species most closely associated with all four rare plants include *Adenostoma fasciculatum*, *Arctostaphylos viscida*, and *Salvia sonomensis*, defined as the *Arctostaphylos viscida* Alliance or the *Arctostaphylos viscida* - *Adenostoma fasciculatum* / *Salvia sonomensis* Association in the Manual of California Vegetation (Sawyer 2009). Wilson et al. (2009) further separated the PHC vegetation into four vegetation types: xeric chaparral, mesic chaparral, woodland, and grassland.

Results presented herein showed strong associations between the rare plant populations and specific vegetation types and indicator species (Figure 1, Table 4), suggesting that using vegetation community data may be a promising method to determine habitat suitability in the field, particularly to identify suitable but unoccupied sites. Further research is needed to determine whether long-lived associated species could be used as indicator species to identify sites in later successional stages where a seedbank may be present. The distribution of these rare plant populations across the different vegetation types identified in the PHC shows that although the species are often found together in the landscape and treated together as a group for conservation planning, they require different microhabitats for successful conservation and may require a matrix of conservation sites at different successional stages.

Disturbance history was a strong predictor of population abundance at occupied sites, confirming the need for active monitoring and management of appropriate disturbance regimes to sustain viable populations of these species. The response of disturbance-dependent species to different types of disturbance may vary based on individual species traits (Menges 2007), such as reproductive strategy (Franklin et al. 2004, Clarke and Dorji 2008) or competitive ability (Moretti et al. 2008). Surprisingly, fire was a strong predictor of population abundance for only one species, *C. stebbinsii*, although all four species are fire-adapted and were expected to be associated with recently burned areas. This may be due to sampling error caused by the current management practice of fire suppression; there are many more cleared areas than burned areas available for sampling within the PHC. Recently burned habitats were limited to a few small accidental ignition sites and several larger controlled burns that were located in areas with little to no surrounding development, whereas clearings for fire breaks were present throughout the entire region. Ayres (2011) reported that *C. stebbinsii* is relatively short-lived and its populations begin to decline before

being shaded out during succession, which may explain its absence on older firebreaks. However, the importance of fire for *C. stebbinsii* despite the greater availability of cleared habitats indicates that mechanical clearing may not be an adequate replacement for fire to sustain populations of this species. The importance of clearing, rather than fire, as a predictor for the other three species should be viewed with caution, and further research into the relative effects of fire and grading as management tools to provide the disturbance required for these species is needed.

Abiotic habitat attributes including topographic position and soil properties were generally poor predictors of species population abundance within the PHC. This was somewhat unexpected because physical gradients are generally considered strong drivers of plant distributions, and studies have shown that the distributions of edaphic-endemic species are influenced by substrate properties (Kruckeberg 1954, Wolf and Harrison 2001). However, biotic community attributes may provide a better representation of the niche than physical gradients alone because they provide an indirect measure of key abiotic attributes (Elmendorf and Moore 2008) while incorporating species interactions that are not captured using abiotic variables alone (Kruckeberg 1954, Veblen and Young 2009). Here, abiotic variables did show a stronger contribution to population abundance models when considered alone, but had reduced explanatory power or were excluded based on AIC model selection when biotic variables were also considered. Furthermore, all surveys in this study were done within the limited geographic area of the PHC. Abiotic variables may better predict the distributions at broader spatial scales, while biotic variables better differentiate microhabitat differences between sites within the PHC.

Spatial population models have been used to understand habitat occupancy patterns of plants in some systems (Boyle et al. 2002), and habitat configuration may be an important predictor of population size and reproductive output of rare plants (Wolf and Harrison 2001). In this study, spatial configuration had only very weak effects in the population abundance models. Habitat area had little relative importance in predicting species abundance; however, I did find significant correlations between habitat area and population patch area for three of the four species, indicating that habitat area played some role in shaping overall population size. The importance of spatial configuration can be masked by site history and successional dynamics in disturbance-driven systems as shown by Hodgson et al. (2009), and spatial configuration may be less important than local habitat attributes in determining local population abundance (Adriaens et al. 2009). However, spatial configuration may still play an important role in long-term species occupancy patterns, even when habitat quality is taken into account (McVinish and Pollet 2013).

Structure, composition and associated species in the vegetation community were the best indicators of habitat quality for the four disturbance-dependent gabbro rare plants evaluated here, indicating that the vegetation classification paradigm may provide the most information about habitat suitability in this system. Vegetation attributes can be relatively easily collected in the field and should be used in habitat assessments when prioritizing sites for conservation. Disturbance history was also an important component of habitat quality at occupied sites; therefore, management of disturbance and successional stage at suitable sites will be an important component of the conservation strategy. Future research should investigate the use of indicator species in the vegetation community as predictors of suitable but unoccupied habitat for these disturbance-dependent rare plants.

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