Terrestrial Arthropods as Indicators of Ecological Restoration Success in Coastal Sage Scrub (California, U.S.A.)

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Abstract

Ecological restoration enjoys widespread use as a technique to mitigate for environmental damage. Success of a restoration project often is evaluated on the basis of plant cover only. Recovery of a native arthropod fauna is also important to achieve conservation goals. I sampled arthropod communities by pitfall trapping in undisturbed, disturbed, and restored coastal sage scrub habitats in southern California. I evaluated arthropod community composition, diversity, and abundance using summary statistics, cluster analysis, and detrended correspondence analysis (DCA) and investigated influence of vegetation on arthropod communities with multiple regression analysis. Arthropod diversity at undisturbed and disturbed sites was greater than at sites that were 5 and 15 years following restoration ($p < 0.05$). Number of arthropod species was not significantly different among undisturbed, disturbed, and restored sites, and two restoration sites had significantly more individuals than other sites. Vegetation at disturbed and undisturbed sites differed significantly; older restorations did not differ significantly from undisturbed sites in diversity, percent cover, or structural complexity. In multiple regression models, arthropod species richness and diversity was negatively related to vegetation height but positively related to structural complexity at intermediate heights. Exotic arthropod species were negatively associated with overall arthropod diversity, with abundance of the earwig *Forficula auricularia* best predicting diversity at comparison (not restored) sites ($r^2 = 0.29$), and abundance of the spider *Dysdera crocata* and the ant *Linepithema humile* predicting diversity at all sites combined ($r^2 = 0.48$). Native scavengers were less abundant at restored sites than all other sites and, with a notable exception, native predators were less abundant as well. DCA of all species separated restored sites from all other sites on the first axis, which was highly correlated with arthropod diversity and exotic arthropod species abundance. Lower taxonomic levels showed similar but weaker patterns, with example families not discriminating between site histories. Vegetation characteristics did not differ significantly between the newly restored site and disturbed sites, or between mature restoration sites and undisturbed sites. In contrast, arthropod communities at all restored sites were, as a group, significantly different from both disturbed and undisturbed sites. As found in other studies of other restoration sites, arthropod communities are less diverse and have altered guild structure. If restoration is to be successful as compensatory mitigation, restoration success standards must be expanded to include arthropods.

Key words: **assessment, bioindicators, coastal sage scrub, ecological restoration, southern California arthropods.**

Introduction

Modern conservation planning increasingly relies on the use of ecological restoration techniques to improve conditions for natural communities. These efforts are both mandated by agencies as compensatory mitigation, and undertaken by land managers to improve conditions on protected lands. As compensatory mitigation, restoration projects often are evaluated only on the establishment of dominant vegetation, a process better known as "revegetation." However, ecological restoration properly should have the goal of recreating the entirety of an ecosystem (National Research Council 1992), including the invertebrate fauna (Majer 1983, 1989; Jansen 1997; Bowler 2000).

Assessing the progress of restoration projects with arthropods has many advantages (Kremen et al. 1993; Finnamore 1996). The short generation times of most arthropods make them ideal to track year-to-year change in a site, while their small size makes them efficient monitors of subtle yet important variations that may influence the quality of a habitat. Arthropods occupy the widest diversity of microhabitats and niches, and play more ecological roles, than any other group of animals. They have diverse body sizes, vagilities, and growth rates. Their large population sizes, reproductive potential, and short generation times allow the collection of statistically significant sample sizes using relatively passive methods with little potential for depleting populations. Arthropod collections can be maintained virtually indefinitely. Among the disadvantages of using arthropods for evaluating restoration success are a paucity of baseline data with which to compare restored sites, limited taxonomic expertise to identify arthropods, a lack of

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natural history information for many species, and limited research linking arthropod communities to vertebrate communities (McGeoch 1998).

Arthropods have been recognized as efficient indicators of ecosystem function and recommended for use in conservation planning (Rosenberg et al. 1986; Kremen et al. 1993; Finnamore 1996) and many researchers have assessed habitat quality and measured habitat differences using arthropods (e.g., Niemelä et al. 1993; Pollet & Grootaert 1996; Rykken et al. 1997; Kitching et al. 2000; Gibb & Hochuli 2002). Arthropod groups have been used to track restoration success in many contexts (Parmenter & MacMahon 1990; Greenslade & Majer 1993; Williams 1993; Andersen & Sparling 1997; Jansen 1997; Peters 1997; Mattoni et al. 2000; Wheater et al. 2000). For example, arthropod communities have been described in the appraisal of strip mine reclamation for over 20 years (Majer 1983; Majer et al. 1984; Parmenter & MacMahon 1990; Holl 1995, 1996; Andersen 1997; Andersen & Sparling 1997). Other studies of restoration success include investigation of soil microarthropods in prairie (Peters 1997), forest litter invertebrates in tropical forest (Jansen 1997), and arthropods in restored riparian woodlands (Williams 1993). This study introduces the technique for use in coastal sage scrub.

The use of arthropods as bioindicators involves a tradeoff between the taxonomic breadth of organisms sampled and specificity to which they are identified. Jansen (1997), Peters (1997), and Williams (1993) keyed a broad range of specimens to order or family, while Andersen (1997) and Holl (1995, 1996) keyed to species for a single family or order. Single families, such as ants, have been identified as indicators of ecosystem recovery, and have been used extensively in the assessment of restoration and reclamation attempts (e.g., Majer 1984; Majer et al. 1984; Andersen 1997; Andersen & Sparling 1997). However, both low-resolution taxonomically-broad and high-resolution taxonomically-narrow approaches have limitations. For broad approaches, failure to determine taxonomic identity below order confounds analysis if families, genera, and species react differently to environmental conditions. In this instance, order-level aggregation obscures variation that may be important to habitat assessment. Conversely, narrow yet taxonomically precise studies may not act well as surrogates for overall diversity—a study of diverse taxa in tropical forest (birds, butterflies, flying beetles, canopy beetles, canopy ants, leaf-litter ants, termites, and soil nematodes) showed that no one taxonomic group served as a sufficient indicator for diversity in others (Lawton et al. 1998). This study employs a high-resolution taxonomically-broad approach through the use of morphospecies (Oliver & Beattie 1993, 1996).

Assessing restoration projects presents a special challenge for the use of arthropods as bioindicators. Because such projects usually involve planting some component of native vegetation, certain taxonomic groups may respond quickly to such efforts. Other arthropods that depend on specific soil conditions may not populate restorations at all. This study attempts to address these two issues pertaining to the use of arthropods as bioindicators of restoration success. First, to what degree does a specific component of the arthropod community composition follow the appropriate provision of native plants? Second, to what extent do taxonomic groups and levels respond similarly to restoration efforts? This second question leads to the identification of groups or species that may be good indicators of community recovery in restored systems.

The relationship between vegetation characteristics and arthropods is important for two reasons. First, the structure of arthropod communities at restored sites may be influenced by the conditions created by the plant community. Studies of old-field succession and restorations have shown a positive relationship between plant species and structural diversity and arthropod diversity (Murdoch et al. 1972; Southwood et al. 1979; Hawkins & Cross 1982; Stinson & Brown 1983; Parmenter & MacMahon 1987, 1990). Second, plant community characteristics are those most often used to measure success of restorations in a regulatory context. This study offers insight into whether such standards for restoration success correspond with development of arthropod communities found in undisturbed sites.

The fine-resolution taxonomically-broad approach to comparing restorations in this study may provide several indicators of success. Arthropod guild structure could be important, and a good indicator of a successful restoration should be rare, predatory arthropods (Peters 1997). Because other studies of guild structure during succession use different sampling measures (*e.g.*, sweep netting, vacuuming) than this study (pitfall trapping), the guild proportions shown in those studies (Teraguchi et al. 1977; Moran & Southwood 1982; Hendrix et al. 1988) are not likely to be replicated. Comparison of guild structure among sites, however, should be illustrative. Exotic arthropods should be an indicator of restoration success or failure. Argentine ants (*Linepithema humile*) have received the most attention as invaders in Mediterranean ecosystems (Erickson 1971; Cole et al. 1992; Holway 1995; Human & Gordon 1997), but several other species (*Armadillidium vulgare* [Isopoda], *Porcellio* spp. [Isopoda], *Forficula auricularia* [Dermaptera], and *Dysdera crocata* [Aranae]) may be important (Paris & Pitelka 1962; Paris 1963; Langston & Powell 1975; Barthell et al. 1998; Bolger et al. 2000). Restored, undisturbed, and disturbed habitats will likely differ in the proportion of exotic species present.

The study reported here allows for investigation of these two issues—the response of terrestrial arthropod communities to restored vegetation, and the suitability of different taxonomic groups and hierarchical levels, and community structure to assess such responses.

Methods

Study Sites

Sites with disturbed, undisturbed, and restored coastal sage scrub were identified on the Palos Verdes Peninsula

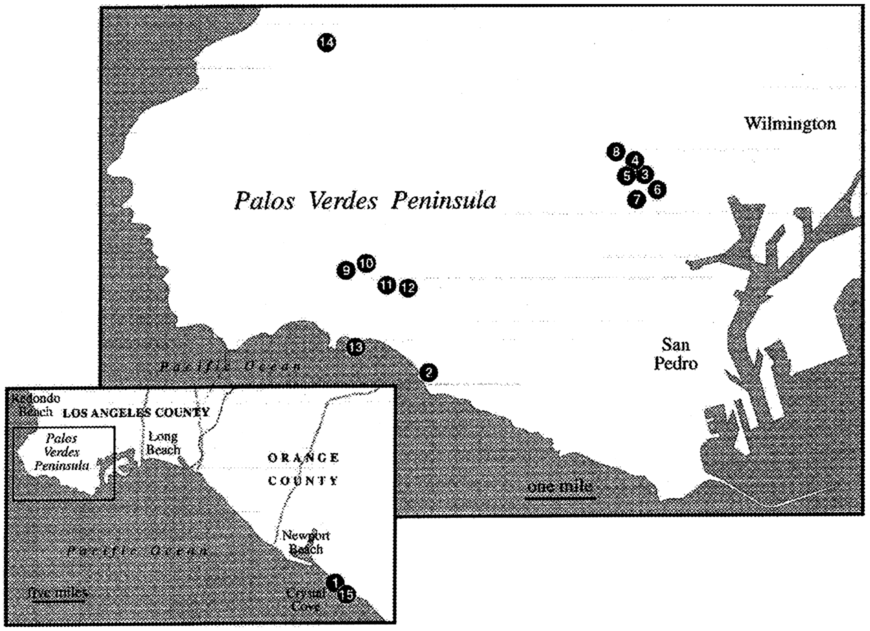

Figure 1. Map of sites studied. (1) Crystal Cove State Park-Pelican Point, (2) Ocean Trails, (3) DFSP-Restoration, (4) DFSP-Office, (5) DFSP-Disaster Shelter, (6) DFSP-Locoweed, (7) DFSP-South End, (8) DFSP-Hill, (9) Kelvin Canyon, (10) Fennel Hill, (11) Portuguese Canyon, (12) Klondike Canyon, (13) Inspiration Point, (14) Malaga Canyon, (15) Crystal Cove State Park-Crystal Cove.

in southwestern Los Angeles County, California, and in coastal Orange County to the south (Fig. 1; Table 1). Coastal sage scrub is a summer deciduous vegetation type dominated by shrubs 0.5–1.5 m and found on the Pacific coast of North America from southern Oregon to northern Mexico (Axelrod 1978; O'Leary 1990). Restoration sites are compared with both disturbed and undisturbed coastal sage scrub ("comparison sites"). All restorations were completed as compensatory mitigation (for details of treatments and dominant vegetation see Table 1). The undisturbed sites provide "reference" conditions sensu White and Walker (1997). Sites were chosen to minimize the effects of size and isolation; all of the restoration sites and most of the comparison sites are contiguous with undisturbed habitat blocks. The overall matrix in the study region is that of urban land use, so none of the sites can be called "pristine." All show signs of degradation from human disturbance, especially the presence of exotic arthropod and plant species. However, the undisturbed sites represent the goal of the restorations within the existing landscape constraints. Disturbed sites are included to investigate whether arthropod communities at restoration sites resemble those in successional habitats.

Sampling Methodology

Pitfall Trapping. I sampled terrestrial arthropod communities monthly with pitfall traps at each restoration and comparison site in 1998 (18 January, 15 February, 19 March, 22 April, 20 May, 24 June, 26 July, 23 August, 27 September, 28 October, 29 November, 29 December). Pitfall traps consisted of two cylindrical plastic containers, each 10 cm across and 13 cm deep, nested together and buried so that the rim of the inner container was flush with the soil. Each trap was covered with a plywood lid, 20 cm square and 0.5 cm thick, supported ~2 cm above the rim by wooden legs. Traps were filled to a depth of 2 cm with ethylene glycol as preservative. Each site was sampled by 2–3 pitfall traps separated by 20 m as topography and vegetation allowed, which should be sufficiently distant to avoid sampling bias (Ward et al. 2001). More than 2 or 3 replicate traps in such proximity at a site previously had been shown to be duplicative in a coastal dune environment (Mattoni et al. 2000). Sites that had traps destroyed by animals or humans during this study were dropped from analysis. Two restoration sites were sampled only from April to December, so most analyses are limited to data from nine months.

All arthropods collected in traps were sorted to family, to genus and species when possible, and otherwise assigned to morphospecies (Oliver & Beattie 1993; Oliver & Beattie 1996). Abundance data to morphospecies level were entered into *Biota*, a relational database designed explicitly for biodiversity data and collection management (Colwell 1996). *EstimateS* (Colwell 1997) was used to calculate species diversity measures.

Each species was assigned to a guild based on available reference materials (Borror & White 1970; White 1983; Borror et al. 1989; Arnett 1993; Hogue 1993). The guilds were phytophage, predator, scavenger, ant, and parasite.

Vegetation Sampling. Vegetation characteristics surrounding each of the 2–3 pitfall trap sample points at each site were measured during spring growth between 7 April and 2 June 1998 by placing a sampling pin at 30 random locations from a 10-m diameter circle around the trap. The 2-m sampling pin was marked at 20-cm intervals. For the first 10 pins, the number of intercepts of each plant species in

Table 1. Restored, disturbed, and undisturbed coastal sage scrub sampling sites, Los Angeles and Orange counties, California.

*Site**	*Dominant Plant Species (>10% cover)*	*Comments*
Undisturbed		
DFSP-Office (4)	California sagebrush, *Artemisia californica* (34%), black mustard, *Brassica nigra* (13%), coyote brush, *Baccharis pilularis* (12%)	High native plant cover, flora not diverse.
DFSP-Disaster Shelter (5)	California sunflower, *Encelia californica* (63%)	High native plant cover, flora not diverse.
DFSP-Locoweed (6)	California sagebrush, *Artemisia californica* (30%), California sunflower, *Encelia californica* (28%), brome, *Bromus* sp. (22%)	High native plant cover, some invasive trees.
Kelvin Canyon (9)	Laurel sumac, *Malosma laurina* (28%), purple sage, *Salvia leucophylla* (25%), California sunflower, *Encelia californica* (17%)	Diverse, mature coastal sage scrub.
Portuguese Canyon (11)	California sunflower, *Encelia californica* (30%), California sagebrush, *Artemisia californica* (19%), burclover, *Medicago* sp. (16%), ashyleaf buckwheat, *Eriogonum cinereum* (14%)	Possibly disturbed in 1940s, now mature scrub.
Klondike Canyon (12)	California sunflower, *Encelia californica* (25%), ashyleaf buckwheat, *Eriogonum cinereum* (17%), purple sage, *Salvia leucophylla* (17%), brome, *Bromus* sp. (15%)	Diverse, mature coastal sage scrub.
Inspiration Point (13)	California sunflower, *Encelia californica* (49%), California sagebrush, *Artemisia californica* (45%)	Farmed in 1920s but now with high native plant cover.
Disturbed		
DFSP-South End (7)	Deerweed, *Lotus scoparius* (24%), brome, *Bromus* sp. (20%), oats, *Avena* sp. (18%), sourclover, *Meliotus indica* (17%), storksbill, *Erodium cicutarium* (12%)	Early succession following construction of drainage channel.
DFSP-Hill (8)	Deerweed, *Lotus scoparius* (23%), storksbill, *Erodium cicutarium* (18%), brome, *Bromus* sp. (13%), oats, *Avena* sp. (12%), iceplant, *Carpobrotus edulis* (11%)	Early succession on fill from construction project completed in 1987.
Fennel Hill (10)	Fennel, *Foeniculum vulgare* (44%), oats, *Avena* sp. (22%), burclover, *Medicago* sp. (14%), brome, *Bromus* sp. (13%)	Probably farmed in past.
Malaga Canyon	Brome, *Bromus* sp. (45%), California rose, *Rosa californica* (15%), goldenbush, *Isocoma menziesii* (13%)	Disturbed by drainage project in 1996.
Restoration		
Crystal Cove (Orange County) (1)	California sunflower, *Encelia californica* (24%), brome, *Bromus* sp. (15%), California sagebrush, *Artemisia californica* (14%)	Farmed through 1900s, seeded with mixture of annual and perennial scrub species in 1985 (see Hillyard 1990).
Pelican Point (Orange County) (1)	California sagebrush, *Artemisia californica* (39%), California buckwheat, *Eriogonum fasciculatum* (16%), black sage, *Salvia mellifera* (13%)	Farmed through 1900s, seeded and planted in 1984 (see Hillyard 1990).
Ocean Trails (2)	California sunflower, *Encelia californica* (42%), brome, *Bromus* sp. (18%), burclover, *Medicago* sp. (13%)	Farmed in early 1900s, fallow until 4.5 acres restored as compensatory mitigation in 1994. Restoration included 1) mowing followed by disking and seeding, 2) disking and seeding, and 3) planting of container stock. Irrigated during plant establishment.
DFSP-Restoration (3)	Brome, *Bromus* sp. (18%), storksbill, *Erodium cicutarium* (16%), deerweed, *Lotus scoparius* (15%), telegraph weed, *Heterotheca grandiflora* (12%)	Prior land use unknown, disturbed for construction of terrace drain. Restoration in 1997 included clearance by hand and installation of container stock. Irrigated in 1997.

*Values in parentheses correspond to the numbers given in Figure 1.
DFSP, Defense Fuel Support Point, located in San Pedro, California.

each of the 10 height classes was recorded. For the remaining 20 pins all species intercepting the pin were recorded. From these data, plant structural complexity was quantified with a height index (Gibson et al. 1987; Hendrix et al. 1988). This index is defined as:

$$\text{height index} = \frac{\sum_{i=1}^{N}(h_i \times n_i)}{\sum_{i=1}^{N}(n_i)} \quad (1)$$

where h = the midpoint of each height class i, n = the number of intercepts at height class i, and N = number of height classes represented by the sample (Hendrix et al. 1988). Plant species intercepts from all 30 locations were used to calculate native species richness, Shannon-Wiener diversity, and the percent native cover.

Statistical Techniques

Differences in arthropod and vegetation variables between trap sample points at all sites were compared using analysis of variance in which trap sample points from undisturbed and disturbed sites were each treated as a group and compared to results from each of the restoration sites using the Tukey-Kramer honest significant difference test (Kramer 1956). For arthropod data, Student's t was used to compare diversity (Fisher's alpha), number of species, and number of individuals. Vegetation variables compared were diversity (Shannon-Wiener), number of intercepts, height index, number of native species, and percent native cover.

Relationships between vegetation and arthropod variables were tested for each of the arthropod variables by building a stepwise multiple regression model with forward entry of vegetation measures. Vegetation measures (number of native plant species, Shannon-Wiener diversity, height index, number of intercepts) were used to create models for arthropod diversity (Fisher's alpha), number of species, and number of individuals. Models were created for undisturbed and disturbed sites alone, and for all sites together to investigate whether arthropod communities in restoration sites responded differently than other sites. To identify the effect of exotic arthropods on overall arthropod diversity, a model was also created to explain arthropod diversity using abundance of exotic arthropod species.

All specimen numbers for the period with complete sampling, April–December 1998, were log transformed to normalize their distribution. Trap sample points and arthropod species were ordinated using detrended correspondence analysis (DCA) (ter Braak 1987–1992, 1996; ter Braak & Prentice 1988). This method assumes an underlying normal distribution of the data in response to environmental variation and reduces the variation to several unrelated axes. Normal response to temporal variation in temperature and precipitation was evident in an analysis of five years of data from the comparison sites (Longcore 1999), so I assumed a normal response curve to spatial variation. Ordination was completed for a series of taxonomic levels: ants (family), tenebrionid beetles (family), beetles (order), spiders (order), insects (class), arachnids (class), arthropods (phylum). Plant abundance data were also log transformed and ordinated using DCA.

Trap sample points were clustered using Ward's agglomerative method with plant and arthropod incidence data as inputs. All statistical tests were performed using JMP statistical software (SAS Institute 1997). Correspondence analysis was completed with CANOCO (ter Braak 1987–1992).

Results

Arthropod Data

The 1,293 trap collections averaged 45.99 ± 40.38 SD specimens of 9.11 ± 3.65 SD species per sample point. The distribution of specimens per collection was not normal because of large specimen counts in some collections. Log transformation normalized the number of specimens per collection.

The species rank abundance curve for the entire collection indicates that the distribution of species follows a log normal distribution (Magurran 1988). Individual sample point rank abundance curves revealed a log series distribution. Based on this species distribution, Fisher's alpha was chosen as the appropriate measure of arthropod diversity, because it assumes an underlying log series distribution. Fisher's alpha has the added advantage of a low sensitivity to sample size (Taylor 1978; Magurran 1988).

Using Fisher's alpha as the appropriate measure of arthropod diversity, the diversity of arthropods at undisturbed sites was greater than the two older restoration sites, Ocean Trails ($p < 0.1$) and Crystal Cove/Pelican Point ($p < 0.05$). DFSP-Restoration was not significantly different. When 12 months of samples were used for the Ocean Trails comparison, confidence increased ($p < 0.05$). The differences in species number were insignificant, with DFSP-Restoration supporting the maximum number of arthropod species and the other two restorations supporting the fewest. DFSP-Restoration and the combined Crystal Cove/Pelican Point restoration sites had significantly more individuals than all other sites (Table 2).

Vegetation Data

Results from vegetation sampling show restorations similar to either disturbed or undisturbed sites depending on the age of the restoration (Table 2). California sagebrush (*Artemisia californica*) and California sunflower (*Encelia californica*) were dominant species at most undisturbed sites and the older restoration sites (Table 1). Sample points from DFSP-Restoration were significantly more diverse than those from the undisturbed sites, and they had significantly fewer plant intercepts than other sites. The

Table 2. Summary statistics for arthropod diversity and abundance by category for April–December 1998 (mean $\pm$ SE, standard error uses a pooled estimate of error variance) and summary vegetation statistics by site history (means $\pm$ SE).

	Disturbed	*Undisturbed*	*DFSP-Restoration*	*Ocean Trails*	*Crystal Cove/ Pelican Point*
Number of trap sites	7	19	3	3	4
Arthropods					
Fisher's alpha	9.56 ± 1.27^{a}	9.49 ± 1.49^{a}	8.75 ± 1.39^{a}	$7.16 \pm 0.88^{b*}$	5.75 ± 0.61^{b}
Total species observed per site	34.14 ± 5.27	32.93 ± 5.47	42.00 ± 6.08	26.00 ± 2.00	29.00 ± 3.92
Mean specimens per trap	43.13 ± 22.19^{a}	38.02 ± 17.64^{a}	124.77 ± 27.69^{b}	31.34 ± 5.14^{a}	105.46 ± 38.29^{b}
Vegetation					
Shannon-Wiener diversity	1.74 ± 0.11^{a}	1.62 ± 0.09^{a}	2.27 ± 0.02^{b}	1.61 ± 0.08^{a}	1.85 ± 0.09^{a}
Number of native species	2.00 ± 0.44^{a}	4.79 ± 0.41^{b}	6.00 ± 0.58^{b}	3.67 ± 0.33^{ab}	6.83 ± 0.70^{b}
Proportion native cover	0.19 ± 0.05^{de}	0.73 ± 0.04^{abc}	0.38 ± 0.03^{bcde}	0.52 ± 0.02^{cd}	0.86 ± 0.05^{ab}
Number of intercepts	146.57 ± 23.81^{ab}	173.74 ± 9.14^{b}	75.33 ± 12.17^{a}	120.67 ± 6.84^{ab}	131.67 ± 7.34^{ab}
Height index	43.22 ± 8.00^{ab}	48.38 ± 2.36^{b}	21.13 ± 1.48^{a}	34.84 ± 3.39^{ab}	51.68 ± 4.33^{b}

Superscripts indicate significantly different groups ($p < 0.05$).
*Significant when 12 samples are compared.

samples from disturbed sites had significantly fewer native plant species than did the undisturbed sites, the Crystal Cove restorations, and DFSP-Restoration. Samples from the Crystal Cove restorations had a significantly larger percent native plant cover than disturbed sites or the other two restorations, while the undisturbed sites had significantly larger percent native cover than disturbed sites and DFSP-Restoration. DCA ordination of vegetation sample points shows that the two older restorations were similar to undisturbed sites, while the one-year-old DFSP-Restoration was similar to disturbed sites (Fig. 2). Ward's method of agglomerative clustering for both plant species and structure data confirmed this result. DFSP-Restoration clustered with the disturbed sites at the first level, with the other restoration sites interspersed with the undisturbed sites.

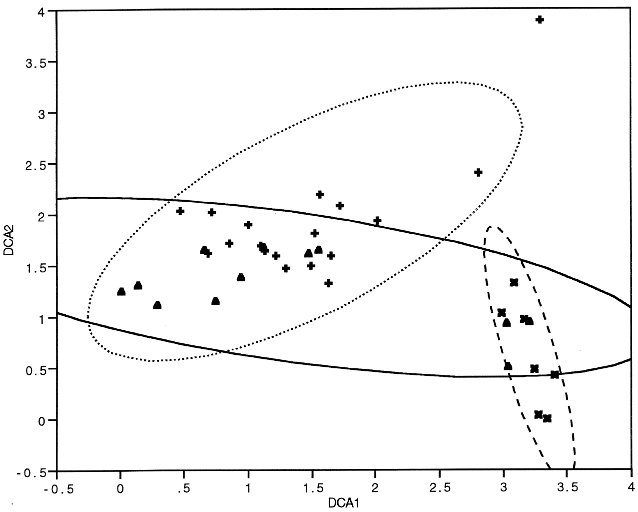

Figure 2. Detrended correspondence analysis of plant communities. Symbols indicate undisturbed (+), disturbed (X), and restored (Δ) sample points. Bivariate ellipses ($p = 0.95$) show clusters of undisturbed (dotted), disturbed (dashed), and restored (solid) coastal sage scrub sites.

Vegetation–Arthropod Relationships

Two vegetation characteristics significantly explained the number of arthropod species found at all sites: 1) more native plant species were associated with more arthropod species, and 2) a greater vegetation height index was associated with fewer arthropod species (Table 3). The number of arthropod individuals had three predictors: vegetation Shannon-Wiener diversity; number of native plant species; and number of intercepts. This relationship is largely an artifact of the superabundance of a few species of exotic arthropods and is not explored further. Arthropod diversity (Fisher's alpha) was predicted by: (1) the number of 40–60 cm height class intercepts; (2) vegetation height index, and (3) percent native cover (Table 3).

Influence of Exotic Arthropods

For undisturbed and disturbed sites, the stepwise multiple regression model for arthropod diversity based on exotic species included one species, the European earwig (*Forficula auricularia*), which explained 29% of the variation in overall arthropod diversity (Table 3). The model including all sites showed significant predictive value for abundance of: (1) Argentine ants (*Linepithema humile*), and (2) the exotic spider *Dysdera crocata*, with an overall model explanation of 48% (Table 3).

Arthropod Guild Composition

Argentine ants dominated the exotic species and guild structure (Table 4), ranging from 5.9 to 54.3% of individuals at sites. Sites with lower percentages of Argentine ants had correspondingly larger proportions of native scavengers. All guilds were represented, but the trapping methodology resulted in a majority of ants, predators, and scavengers, rather than phytophages. Percentage native predators

Table 3. Stepwise multiple regression models for arthropod species richness and diversity by vegetation characteristics (I and II) and exotic arthropod abundance (III and IV).

Model (r^2)	*Variable*	*Coefficient*	*Standard Error*	*T score*	*p Value*
I. Arthropod species richness, all sites by vegetation characteristics (0.48)	Intercept	47.25	2.96	15.96	<0.0001
	Number native plant species	1.12	0.35	3.19	0.004
	Vegetation height index	−0.17	0.05	−3.24	0.004
II. Arthropod diversity, all sites by vegetation characteristics (0.66)	Intercept	12.05	0.92	13.03	<0.0001
	Plant intercepts 40–60 cm	0.09	0.03	3.47	0.0022
	Vegetation height index	−0.08	0.02	−4.88	<0.0001
	Percent native cover	2.06	0.87	2.37	0.027
III. Arthropod diversity, comparison sites, by exotic arthropod abundance (0.29)	Intercept	13.13	0.49	26.97	<0.0001
	Forficula auricularia	−1.89	0.61	−3.10	0.005
IV. Arthropod diversity, all sites, by exotic arthropod abundance (0.48)	Intercept	10.73	0.46	23.25	<0.0001
	Dysdera crocata	−2.61	1.46	−1.79	0.085
	Linepithema humile	−1.03	0.31	−3.34	0.002

ranged from 5.1 to 41.0%. The extremely high value for predators at Ocean Trails resulted from an abundance of spiders. Mean percentages for each native guild were lower in restorations than undisturbed sites. The lower percentages of native guilds are especially apparent for native scavengers, which were less prevalent at restored sites. With the exception of spiders at Ocean Trails, native predators constituted a significantly smaller proportion of captures at restorations than at undisturbed sites.

Cluster Analysis

Cluster analysis of sample points based on arthropod species formed three large clusters: (1) sample points from all three restorations, (2) sample points from DFSP-Hill and DFSP-South End (both disturbed); and (3) sample points from all other sites (Fig. 3). Seven of 14 sets of sample points from the same site formed exclusive clusters and all terminal pairs but one were made up of sample points from the same site. Of the disturbed sites, Fennel Hill clustered with undisturbed sites. The greater height of vegetation at Fennel Hill influences its arthropod community. As shown below, the sample points from non-restoration sites are separated by differences in vegetation height.

When exotic arthropods were removed from the clustering analysis, the distinctions between restorations, disturbed, and undisturbed sites largely remained. There were two interesting differences. First, DFSP-Restoration sample

Table 4. Mean percentage of arthropods by guild and nativity at undisturbed, disturbed, and restored coastal sage scrub sites.

Site	*Exotic Ant (%)*	*Exotic Phyt (%)*	*Exotic Pred (%)*	*Exotic Scav (%)*	*Total Exotic (%)*	*Native Ant (%)*	*Native Para (%)*	*Native Phyt (%)*	*Native Pred (%)*	*Native Scav (%)*
Undisturbed										
DFSP-Office	28.3	0.1	0.5	14.2	43.1	0.8	0.4	8.3	29.5	17.9
DFSP-Locoweed	24.5	0.0	0.4	15.7	40.6	0.4	0.7	9.8	18.4	30.1
DFSP-Disaster	17.3	0.0	0.4	11.0	28.8	0.5	1.3	9.4	18.7	41.4
Kelvin Canyon	13.1	0.0	1.0	27.6	41.7	0.7	0.2	4.0	27.7	25.7
Klondike Canyon	22.6	0.1	0.6	16.7	40.0	0.1	0.8	5.4	11.8	41.9
Portuguese Canyon	20.7	0.0	0.4	10.0	31.1	0.7	0.5	7.6	24.9	35.2
Inspiration Point	7.0	0.2	0.7	19.9	27.9	0.1	0.6	3.8	27.7	39.8
Disturbed										
Fennel Hill	23.2	0.0	0.8	27.1	51.1	0.1	0.8	3.2	11.1	33.8
Malaga Canyon	14.1	0.0	0.4	4.4	18.9	0.4	0.1	11.6	25.8	43.3
DFSP-Hill	7.1	0.0	0.2	19.7	27.0	0.3	0.6	5.5	14.7	51.9
DFSP-South End	5.9	0.0	0.2	12.0	18.1	15.9	0.2	2.0	21.1	42.7
Restoration										
Pelican Point	54.3	0.0	1.4	28.5	84.2	0.0	0.0	8.1	5.1	2.5
Crystal Cove	40.6	0.0	0.4	22.8	63.8	2.7	0.3	7.7	12.6	12.8
Ocean Trails	21.0	0.0	1.2	13.0	35.3	0.0	0.4	3.4	41.0	20.0
DFSP-Restoration	15.3	0.0	0.1	38.2	53.6	12.4	0.4	2.5	9.2	21.8

Guilds are ants (Ant), phytophages (Phyt), predators (Pred), parasites (Para), and scavengers (Scav).

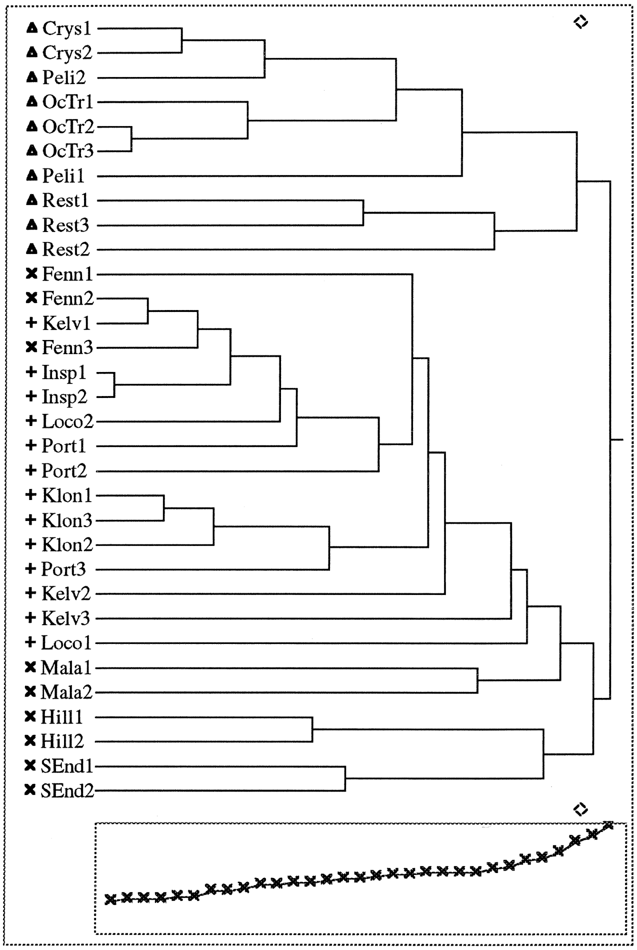

Figure 3. Cluster analysis of sites based on arthropod data. Sites with missing months are omitted as described above. Note that all restorations are separated from other sites at first division. The plot beneath the dendrogram indicates on the ordinate the distance that was bridged to join the clusters at each step. Symbols at left indicate undisturbed (+), disturbed (X), and restored (Δ) trap sample points.

points clustered with the other disturbed sites at DFSP, rather than with the other restorations. Second, one of the DFSP-Locoweed sample points clustered with the restorations at Crystal Cove.

Detrended Correspondence Analysis

Detrended correspondence analysis of vegetation separated disturbed and undisturbed coastal sage sites on the first axis (Fig. 2). Restoration sites, however, overlapped both disturbed and undisturbed sites. The second axis was correlated with vegetation height. The pattern for arthropods was distinctly different. DCA of all arthropod species separated restoration from undisturbed and disturbed sites on the first axis (Fig. 4A). Restorations had significantly ($p < 0.01$) higher scores on the first axis than undisturbed and disturbed sites and, although not as pronounced, disturbed sites had significantly ($p < 0.05$) higher scores than undisturbed sites. A linear regression showed the first axis to be significantly negatively correlated with arthropod diversity ($r^2 = 0.46$, $p < 0.0001$) and positively correlated with abundance of most exotic species. The second axis separated early succession disturbed sites from other undisturbed sites along a height gradient and was significantly correlated with the height index of the vegetation ($r^2 = 0.54$, $p < 0.0001$). Similar patterns were evident in DCA for other taxonomic groups and levels (Fig. 4B–F). In each ordination, restoration sites received significantly different scores on the first axis ($p < 0.05$) than disturbed or undisturbed sites. At the family level, tenebrionid beetles produced overlapping distributions of restored, disturbed, and undisturbed sites. At the class level, spiders and beetles produced similar patterns, separating restored from other sites on the first axis. At the order level, insects showed more difference between restored and other sites, while arachnids showed less difference.

Discussion

Of the restoration sites sampled, none had developed an arthropod community that resembled undisturbed or disturbed native coastal sage scrub. Restoration sites in general exhibited lower arthropod diversity and a preponderance of exotic arthropod species. The time elapsed since revegetation effort had no discernable effect on arthropod community structure; there was no gradual return of the community to a more natural structure over time. Conversely, the oldest revegetation, Crystal Cove State Park, was dominated by exotic arthropods and exhibited extremely low native arthropod diversity.

Vegetation variables explained a substantial portion (48 to 66%) of the variation in arthropod diversity at undisturbed and disturbed sites, but not at restorations. Consistent with succession theory, arthropod diversity increased with vegetation height and complexity. Southwood et al. (1979) described increasing insect taxonomic diversity with increases in plant taxonomic and spatial diversity, followed by a decrease in insect taxonomic diversity with even higher spatial diversity but decreasing plant taxonomic diversity. Southwood et al. (1979) described this relationship as an "arch" in insect taxonomic diversity during succession. When including the disturbed sites on the continuum of height indices documented in the study, there is an arch in arthropod species diversity with the height of vegetation.

More plant intercepts (i.e., greater complexity) at 40 to 60 cm above the ground correlated with higher arthropod diversity, while complexity at heights >60 cm (and a correspondingly greater height index) correlated with lower arthropod diversity. Southwood et al.'s (1979) other predictor, plant diversity, was not found to be significant, but rather percent native cover emerged as a significant predictor of overall arthropod diversity at undisturbed and disturbed coastal sage scrub sites.

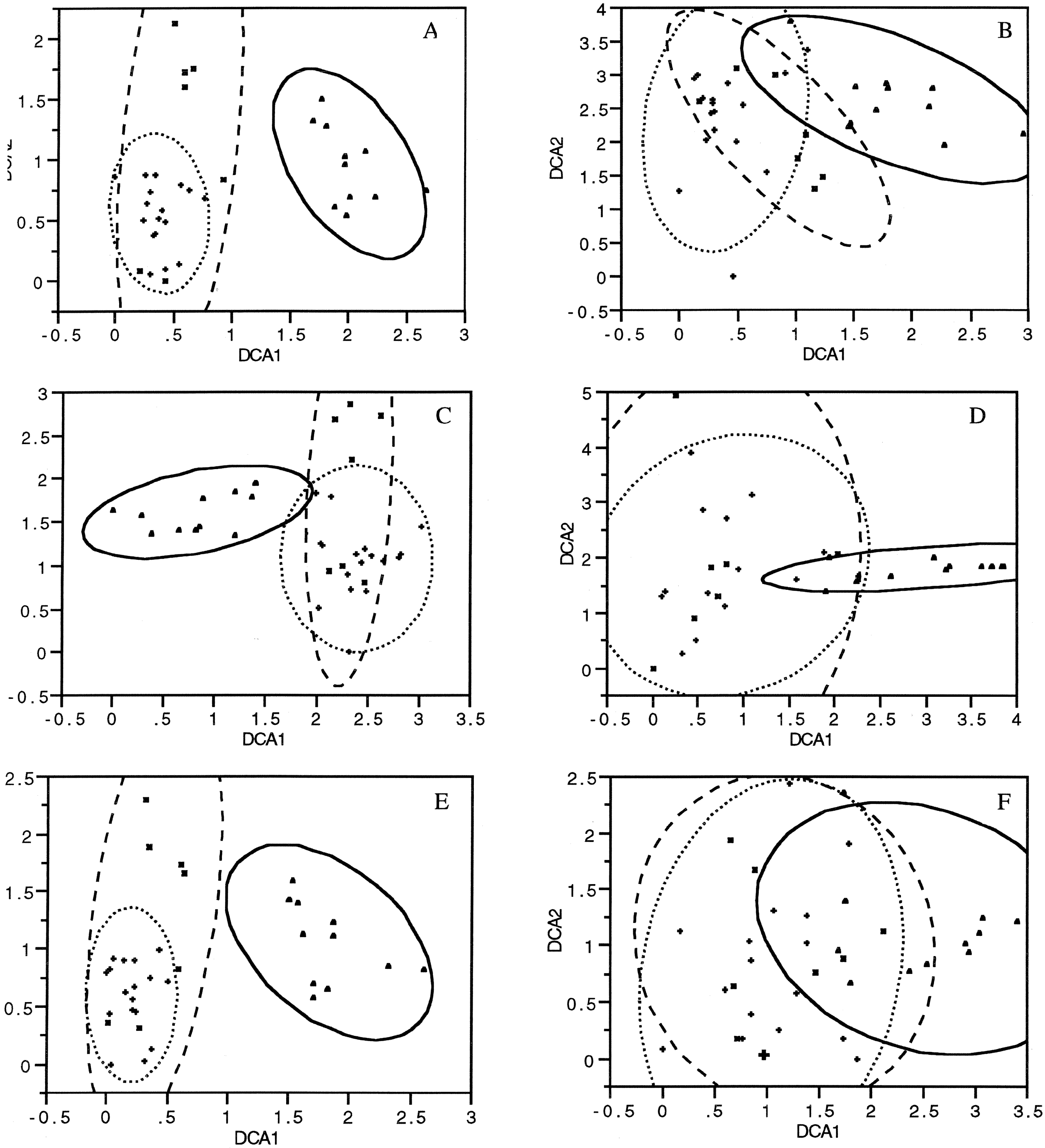

Figure 4. Detrended correspondence analysis of sites based on (A) all species (Arthropoda), (B) darkling beetles (Tenebrionidae), (C) beetles (Coleoptera), (D) spiders (Araneae), (E) insects (Insecta), and (F) arachnids (Arachnida). Symbols indicate undisturbed (+), disturbed (X), and restored (Δ) trap sample points. Bivariate ellipses ($p = 0.95$) show clusters of undisturbed (dotted), disturbed (dashed), and restored (solid) coastal sage scrub sites.

Table 5. Abundance of arthropod species and families with significant differences between undisturbed and disturbed coastal sage scrub sites for 1994–1998 (Longcore 1999).

Taxon	*N*	*Undisturbed*	*p*	*Disturbed*	*Restored*
Ctenizidae					
(Ctenizidae) sp. 1	62	0.063 ± 0.042	**	0.002 ± 0.006	0
Pholcidae					
(Pholcidae) sp. 1	95	0.016 ± 0.008	**	0.152 ± 0.091	0.037
Vejovidae	264	0.281 ± 0.134	***	0.052 ± 0.054	0.044
Paruroctonus silvestrii	240	0.256 ± 0.124	***	0.049 ± 0.048	0.044
Solfugae					
Eremobates sp. 1	227	0.090 ± 0.035	***	0.232 ± 0.074	0.205
Scolopendridae					
Scolopendra sp. 1	45	0.012 ± 0.007	***	0.047 ± 0.032	0.066
Entomobryidae					
(Entomobryidae) sp. 1	1580	0.341 ± 0.247	**	1.919 ± 1.407	2.176
Curculionidae					
Trigonoscuta sp. 1	43	0.040 ± 0.023	**	0.007 ± 0.011	0
Ptinidae					
Ptinus fur	129	0.100 ± 0.082	**	0.013 ± 0.016	0.176
Staphylinidae	1114	1.165 ± 0.472	***	0.202 ± 0.040	0.110
Tenebrionidae					
Coniontis sp. 1	191	0.041 ± 0.015	**	0.322 ± 0.228	0.066
Cratidus osculans	1635	0.676 ± 0.390	**	2.136 ± 0.934	0.728
Nyctoporis carinata	1594	1.585 ± 0.508	***	0.096 ± 0.030	0.904
Forficulidae					
Forficula auricularia	3158	1.102 ± 0.208	***	3.169 ± 0.639	5.154
Polyphagidae					
Arenivaga sp. 1	391	0.367 ± 0.066	***	0.096 ± 0.039	0.044
Anthomyiidae					
(Anthomyiidae) sp. 1	148	0.014 ± 0.010	**	0.265 ± 0.216	0
Reduviidae					
(Reduviidae) sp. 2	43	0.044 ± 0.028	**	0.011 ± 0.011	0
Formicidae					
Pheidole sp. 1	170	0.009 ± 0.009	***	0.195 ± 0.169	0.485
Gryllacrididae					
Stenopelmatus sp. 1	569	0.489 ± 0.146	**	0.256 ± 0.103	0.154
Gryllidae	201	0.190 ± 0.062	****	0.034 ± 0.018	0.063
Hoplosphyrum boreale	179	0.177 ± 0.064	****	0.019 ± 0.019	0.051

Values are means ± standard deviation of 5 yearly mean abundance values. Significance values indicated as ** $p < 0.05$, *** $p < 0.01$, and **** $p < 0.001$. Yearly mean abundance for restored sites (1 year only and therefore without standard deviation) are provided for comparison.

For restoration sites, neither the percent native cover nor the number of native plant species was correlated with increased arthropod species richness or diversity. To the contrary, because of the high native plant cover of the Crystal Cove restorations and their equally low arthropod diversity, the relationship was the opposite of this. Furthermore, all of the restoration sites supported plant communities similar in species incidence and abundance to comparison sites. Vegetation at DFSP-Restoration was similar to the early succession disturbed sites. However similar their vegetation to either disturbed or undisturbed comparison sites, the restoration sites did not support similar arthropod communities, as shown by cluster analysis and DCA.

Exotic arthropod species were important determinants of overall arthropod diversity. This effect was not uniform among undisturbed, disturbed, and restoration sites. For undisturbed and disturbed sites, one exotic species, *Forficula auricularia*, explained 28% of the variance in arthropod diversity. However, for all sites combined, two exotic species, *Dysdera crocata* and *Linepithema humile*, explained 48% of the variance in overall arthropod diversity. This illustrates that the negative correlation between exotic species abundance and overall arthropod diversity is much stronger at restoration sites. This response is probably not the result of the invasion itself, but rather the site conditions that promote the overwhelming abundance of exotic species. Because even the most diverse of the undisturbed sites had been invaded by exotic species, the difference in community structure between them and the restoration sites cannot be attributed to the presence alone of the exotics. Rather, it is likely that a history of intense disturbance and the absence of any remnant native arthropod community allows exotic species to dominate the habitat. The abundant presence of exotic arthropods inhibits invasion of the restoration by native arthropod species from adjacent source areas. This scenario is consistent with the application of assembly rules by which different stable communities depend on the order of species invasion (Diamond 1975; Gilpin 1987). In contrast, the relatively high native arthropod diversity at DFSP-Restoration in the face of rather high exotic species abundance reflects both its history of light disturbance and the avoidance of restoration techniques that would disrupt the native arthropod community (e.g., no grading, hand clearing, and little irrigation).

In addition to the overall differences in arthropod diversity and exotic species abundance between native and restored sites, several species were not found at restoration sites, and these may serve as indicator species. In an analysis of 5 years of collection data from the disturbed and undisturbed sites described here, several predator species and families had significantly different abundance between undisturbed and disturbed sites (Table 5) (Longcore 1999). Undisturbed sites had significantly more scorpions, mostly *Paruroctonus sylvestrii* ($p < 0.01$), and significantly fewer solpugids, *Eremobates* sp. ($p < 0.01$). While predatory themselves, *Eremobates* are a recorded prey species of *Paruroctonus* (Polis & Sissom 1990). Other species and groups that were significantly ($p < 0.01$) different between disturbed and undisturbed sites include staphylinid beetles, the tenebrionid beetle *Nyctoporis carinata*, the exotic earwig *Forficula auricularia*, and sand roaches (*Arenivaga* sp.). Results from restorations in this study were consistent with these findings. Stripe-tailed scorpions (*Paruroctonus silvestrii*) were only found in small numbers at each of the restorations. Another unique predator, the trap door spider (*Aposticus* sp.), was found almost exclusively at undisturbed sites, but with a few records from the restoration at Pelican Point. For other predators, pseudoscorpions or assassin bugs were not found at restoration sites, but were found at undisturbed sites. In addition, although not a predator, the sand roach (*Arenivaga* sp.) was found almost exclusively at undisturbed sites, with only one individual found at the Ocean Trails restoration.

Despite the number of predator species missing from the sampled restorations, the restorations do have predators, but the pattern of predator abundance is not uniform among restorations. At Ocean Trails, 41% of the individuals captured were predators, mostly lycosid spiders. At Crystal Cove, 12.6% of sampled individuals were predators, but only 5.1% were predators at Pelican Point. The DFSP restoration had 9.2% predators. The abundance of individuals of small predator species (spiders) may be the result of the absence of larger predators (e.g., scorpions). Polis and others have described the dynamics of interference, usually predation, among potentially competing species (intraguild predation) (Polis & McCormick 1986; Polis et al. 1989; Holt & Polis 1997). In experimental manipulations, removal of scorpions resulted in a doubling in spider number (Polis & McCormick 1986). Release from intraguild predation is a promising explanation for spider abundance in restoration sites. Similarly, the lack of intraguild predation likely explains the abundance of spiders found at old, isolated scrub fragments by Bolger et al. (2000). Lack of intraguild predation of lycosid spiders by scorpions is an alternative hypothesis to their suggestion that a more productive detrital food web explains high spider abundance in old, isolated fragments (Bolger et al. 2000).

There is some skepticism about the choice of specific taxonomic groups as indicators of disturbance, diversity, or ecosystem health (Andersen 1999). Andersen suggests that some researchers assert that a taxon has indicator qualities because they work on them, not the other way around. McGeoch (1998) has presented an outline by which the indicator qualities of a specific group are validated. Good ecological indicators respond in ways that reflect other taxonomic groups so that efficient methods of assessing change can be implemented. For the current study, two of the orders, beetles and spiders, could have served as indicators for the whole. Arachnids, however, would have been a poor choice and a single family would have been too narrow. For example, tenebrionid beetles only weakly showed the differences between sites. Rykken et al. (1997) similarly found that a beetle family was not a good indicator of ecological type. Ants did not work as indicators because Argentine ants, which reduce native ant diversity, had invaded all sites. DCA of ants did not distinguish between disturbed and undisturbed sites. Beetles as a whole, however, most resembled the response of all arthropods to restoration.

The observed disconnection between vegetation characteristics and terrestrial arthropod communities at restoration sites is troubling. Restoration practitioners usually operate with the attitude that if the plant community is restored, animals will return—"If you build it, they will come" (an expression modified from Kinsella 1982) but this study joins others that show that revegetation does not result in the development of a native arthropod fauna. In a 12-year study of a restored agricultural field, Van Dijk (1986) found little colonization by carabid beetles from the surrounding heathland. Parmenter's series of reports on the development of arthropod communities in a shrub-steppe habitat following mine reclamation found lower species richness, diversity, and evenness up to six years following revegetation compared to control sites (Parmenter & MacMahon 1987, 1990; Parmenter et al. 1991). Parmenter and MacMahon (1987) conclude that the severity of disturbance from mining may preclude forever development of a similar flora and fauna on the site. Williams (1993) showed that restored riparian willow forests supported fewer individuals overall, as well as fewer predators and parasites. Blake et al. (1996) found that 5 years after restoration the carabid beetle fauna of wildflower meadows was characterized by fewer species, lower diversity, and smaller body sizes than undisturbed sites. In another single-family study, ant communities were compared on rehabilitated sand mines ranging from 2 to 20 years since revegetation. While restored sites supported diverse ant communities, the fauna was not similar in species composition to control sites, even after 20 years (Bisevac & Majer 1999).

As ecological restoration is used for compensatory mitigation (i.e. for replacement of natural communities lost through human activity), care should be taken to ensure that arthropod communities are recreated as well. For the restoration sites in this study, none supported an arthropod community similar to undisturbed conditions. However, because of the largely native plant community and percent cover, each would have been considered sufficient under most current regulatory schemes. Restoration standards must be expanded to include measures of arthropod community structure or diversity or land managers and regulators risk the long-term erosion of native diversity through the replacement of native habitats by depauperate imitations.

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LITERATURE CITED

Andersen, A. N. 1997. Using ants as bioindicators: multiscale issues in ant community ecology. Conservation Ecology (online) **1:**8.

Andersen, A. N. 1999. My bioindicator or yours? Making the selection. Journal of Insect Conservation **3:**61–64.

Andersen, A. N., and G. P. Sparling. 1997. Ants as indicators of restoration success: relationship with soil microbial biomass in the Australian seasonal tropics. Restoration Ecology **5:**109–114.

Arnett, R. H., Jr. 1993. American insects. Sandhill Crane Press, Gainesville, Florida.

Axelrod, D. I. 1978. The origin of coastal sage vegetation, Alta and Baja California. American Journal of Botany **65:**1117–1131.

Barthell, J. F., G. W. Frankie, and R. W. Thorp. 1998. Invader effects in a community of cavity nesting megachilid bees (Hymenoptera: Megachilidae). Environmental Entomology **27:**240–247.

Bisevac, L., and J. D. Majer. 1999. Comparative study of ant communities of rehabilitated mineral sand mines and heathland, Western Australia. Restoration Ecology **7:**117–126.

Blake, S., G. N. Foster, G. E. J. Fisher, and G. L. Ligertwood. 1996. Effects of management practices on the carabid faunas of newly established wildflower meadows in southern Scotland. Annales Zoologici Fennici **33:**139–147.

Bolger, D. T., A. V. Suarez, K. R. Crooks, S. A. Morrison, and T. J. Case. 2000. Arthropods in urban habitat fragments in southern California: area, age and edge effects. Ecological Applications **10:** 1230–1248.

Borror, D. J., C. A. Triplehorn, and N. F. Johnson. 1989. An introduction to the study of insects. 6th ed. Saunders College Publishing, New York.

Borror, D. J., and R. E. White. 1970. A field guide to the insects: America north of Mexico. Edited by R. T. Peterson. Vol. 19, The Peterson field guide series. Houghton Mifflin, Boston.

Bowler, P. A. 2000. Ecological restoration of coastal sage scrub and its potential role in habitat conservation plans. Environmental Management **26:**S85–S96.

Cole, F. R., A. C. Medeiros, L. L. Loope, and W. W. Zuehlke. 1992. Effects of the Argentine ant on arthropod fauna for Hawaiian high-elevation shrubland. Ecology **73:**1313–1322.

Colwell, R. K. 1996. Biota: the biodiversity database manager. Sinauer, Sunderland, Massachusetts.

Colwell, R. K. 1997. EstimateS: statistical estimation of species richness and shared species from samples. User's Guide and application published at http://viceroy.eeb.uconn.edu/estimates. University of Connecticut, Storrs.

Diamond, J. M. 1975. The assembly of species communities. Pages 342–444 in M. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belnap & Harvard University Press, Cambridge.

Erickson, J. M. 1971. The displacement of native ant species by the introduced Argentine ant *Iridomyrmex humilis* (Mayr). Psyche **78:**257–266.

Finnamore, A. T. 1996. The advantages of using arthropods in ecosystem management. Biological Survey of Canada (Terrestrial Arthropods) for Canadian Museum of Nature and Entomological Society of Canada, Ottawa.

Gibb, H., and D. F. Hochuli. 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biological Conservation **106:**91–100.

Gibson, C. W. D., H. C. Dawkins, V. K. Brown, and M. Jepson. 1987. Spring grazing by sheep: effects on seasonal changes during old field succession. Vegetatio **70:**33–43.

Gilpin, M. E. 1987. Experimental community assembly: competition, community structure and the order of species introductions. Pages 151–161 in W. R. Jordan, III, M. E. Gilpin and J. D. Aber, editors. Restoration ecology: a synthetic approach to ecological research. Cambridge University Press, Cambridge.

Greenslade, P., and J. D. Majer. 1993. Recolonization by collembola of rehabilitated bauxite mines in Western Australia. Australian Journal of Ecology **18:**385–394.

Hawkins, B. A., and E. A. Cross. 1982. Patterns of refaunation of reclaimed strip mine spoils by nonterricolous arthropods. Environmental Entomology **11:**762–775.

Hendrix, S. D., V. K. Brown, and H. Dingle. 1988. Arthropod guild structure during early old field succession in a New World and Old World site. Journal of Animal Ecology **18:**301–310.

Hillyard, D. 1990. Coastal sage scrub restoration in Orange County: two approaches. Pages 20–25 in P. J. Bryant and J. Remington, editors. Endangered wildlife and habitats in southern California. Natural History Foundation of Orange County, Newport Beach, California.

Hogue, C. L. 1993. Insects of the Los Angeles basin. Natural History Museum of Los Angeles County, Los Angeles.

Holl, K. D. 1995. Nectar resources and their influence on butterfly communities on reclaimed coal surface mines. Restoration Ecology **3:**76–85.

Holl, K. D. 1996. The effect of coal surface mine reclamation on diurnal lepidopteran conservation. Journal of Applied Ecology **33:**225–236.

Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist **149:**745–764.

Holway, D. A. 1995. Distribution of the Argentine ant (*Linepithema humile*) in northern California. Conservation Biology **9:**1634–1637.

Human, K. G., and D. M. Gordon. 1997. Effects of Argentine ants on invertebrate biodiversity in northern California. Conservation Biology **11:**1242–1248.

Jansen, A. 1997. Terrestrial invertebrate community structure as an indicator of the success of a tropical rainforest restoration project. Restoration Ecology **5:**115–124.

Kinsella, W. P. 1982. Shoeless Joe. Ballantine Books, New York.

Kitching, R. L., A. G. Orr, L. Thalib, H. Mitchell, M. S. Hopkins, and A. W. Graham. 2000. Moth assemblages as indicators of environmental quality in remnants of upland Australian rain forest. Journal of Applied Ecology **37:**284–297.

Kramer, C. Y. 1956. Extension of multiple range tests to group means with unequal number of replications. Biometrics **12:**309–310.

Kremen, C., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss, and M. A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. Conservation Biology **7:**796–808.

Langston, R. L., and J. A. Powell. 1975. The earwigs of California (Order Dermaptera). Bulletin of the California Insect Survey **20:**1–25.

Lawton, J. H., D. E. Bignell, B. Bolton, G. F. Bloemers, P. Eggleton, P. M. Hammond, M. Hodda, R. D. Holt, T. B. Larsen, N. A. Mawdsley, N. E. Stork, D. S. Srivastava, and A. D. Watt. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature **391:**72–76.

Longcore, T. R. 1999. Terrestrial arthropods as indicators of restoration success in coastal sage scrub. Ph.D. thesis, Department of Geography, University of California, Los Angeles.

Magurran, A. E. 1988. Biological diversity and its measurement. Princeton University Press, Princeton, New Jersey.

Majer, J. D. 1983. Bio-indicators of minesite rehabilitation, land use and land conservation. Environmental Management **7:**375–383.

Majer, J. D. 1984. Recolonization by ants in rehabilitated open-cut mines in northern Australia. Reclamation & Revegetation Research **2:**279–298.

Majer, J. D., editor. 1989. Animals in primary succession: the role of fauna in reclaimed lands. Cambridge University Press, Cambridge.

Majer, J. D., J. E. Day, E. D. Kabay, and W. S. Perriman. 1984. Recolonization by ants in bauxite mines rehabilitated by a number of different methods. Journal of Applied Ecology **51:**289–306.

Mattoni, R., T. Longcore, and V. Novotny. 2000. Arthropod monitoring for fine scale habitat analysis: a case study of the El Segundo dunes. Environmental Management **25:**445–452.

McGeoch, M. A. 1998. The selection, testing and application of terrestrial insects as bioindicators. Biological Reviews (Cambridge) **73:**181–201.

Moran, V. C., and T. R. E. Southwood. 1982. The guild composition of arthropod communities in trees. Journal of Animal Ecology **51:**289–306.

Murdoch, W. W., F. C. Evans, and C. H. Peterson. 1972. Diversity and pattern in plants and insects. Ecology **53:**819–829.

National Research Council. 1992. Restoration of aquatic ecosystems: science, technology, and public policy. National Research Council, Washington, DC.

Niemelä, J., D. Langor, and J. R. Spence. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. Conservation Biology **7:**551–561.

O'Leary, J. F. 1990. California coastal sage scrub: general characteristics and considerations for biological conservation. Pages 24–41 in A. A. Schoenherr, editor. Endangered plant communities of southern California. Southern California Botanists, Claremont, California.

Oliver, I., and A. J. Beattie. 1993. A possible method for the rapid assessment of biodiversity. Conservation Biology **7:**562–568.

Oliver, I., and A. J. Beattie. 1996. Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. Ecological Applications **6:**594–607.

Paris, O. H. 1963. The ecology of *Armadillidium vulgare* (Isopoda: Oniscoidea) in California grassland: food, enemies, and weather. Ecological Monographs **33:**1–22.

Paris, O. H., and F. A. Pitelka. 1962. Population characteristics of the terrestrial isopod *Armadillidium vulgare* in California grassland. Ecology **43:**229–248.

Parmenter, R. R., and J. A. MacMahon. 1987. Early successional patterns of arthropod recolonization on reclaimed strip mines in southwestern Wyoming: the ground-dwelling beetle fauna (Coleoptera). Environmental Entomology **16:**168–177.

Parmenter, R. R., and J. A. MacMahon. 1990. Faunal community development on disturbed lands: an indicator of reclamation success. Pages 73–89 in J. C. Chambers and G. L. Wade, editors. Evaluating reclamation success: the ecological consideration. USDA, Forest Service, Northeastern Forest Station, Radnor, Pennsylvania.

Parmenter, R. R., J. A. MacMahon, and C. A. B. Gilbert. 1991. Early successional patterns of arthropod recolonization on reclaimed Wyoming strip mines: the grasshoppers (Orthoptera: Acrididae) and allied faunas (Orthoptera: Gryllacrididae, Tettigoniidae). Environmental Entomology **20:**135–142.

Peters, J. R. 1997. Soil microarthropod possible indicators of prairie recovery (Illinois). Restoration & Management Notes **15:**78–79.

Polis, G. A., and S. J. McCormick. 1986. Scorpions, spiders and solpugids: predation and competition among distantly related taxa. Oecologia **71:**111–116.

Polis, G. A., C. A. Meyers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics **20:**297–330.

Polis, G. A., and W. D. Sissom. 1990. Life history. Pages 161–223 in G. A. Polis, editor. The biology of scorpions. Stanford University Press, Stanford, California.

Pollet, M., and P. Grootaert. 1996. An estimation of the natural value of dune habitats using Empidoidea (Diptera). Biodiversity and Conservation **5:**859–880.

Rosenberg, D. M., H. V. Danks, and D. M. Luhmkuhl. 1986. Importance of insects in environmental impact assessment. Environmental Management **10:**773–783.

Rykken, J. J., D. E. Capen, and S. P. Mahabir. 1997. Ground beetles as indicators of land type diversity in the green mountains of Vermont. Conservation Biology **11:**522–530.

SAS Institute. 1997. JMP Statistical Discovery Software 3.2. SAS Institute, Inc., Cary, North Carolina.

Southwood, T. R. E., V. K. Brown, and P. M. Reader. 1979. The relationships of plant and insect diversities in succession. Biological Journal of the Linnean Society **12:**327–348.

Stinson, C. S. A., and V. K. Brown. 1983. Seasonal changes in the architecture of natural plant communities and its relevance to insect herbivores. Oecologia **56:**67–69.

Taylor, L. R. 1978. Bates, Williams, Hutchinson—a variety of diversities. Pages 1–18 in L. A. Mound and N. Waloff, editors. Diversity of insect faunas: 9th symposium of the Royal Entomological Society. Blackwell, Oxford.

ter Braak, C. J. F. 1987–1992. CANOCO—a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis. Microcomputer Power, Ithaca, New York.

ter Braak, C. J. F. 1996. Unimodal models to relate species to environment. DLO-Agricultural Mathematics Group, Wageningen.

ter Braak, C. J. F., and I. Prentice. 1988. A theory of gradient analysis. Advances in Ecological Research **18:**271–317.

Teraguchi, S., M. Teraguchi, and R. Upchurch. 1977. Structure and development of insect communities in an Ohio old-field. Environmental Entomology **6:**247–257.

Van Dijk, T. S. 1986. Changes in the carabid fauna of a previously agricultural field during the first twelve years of impoverishing treatments. Netherlands Journal of Zoology **36:**413–437.

Ward, D. F., T. R. New, and A. L. Yen. 2001. Effects of pitfall trap spacing on the abundance, richness and composition of invertebrate catches. Journal of Insect Conservation **5:**47–53.

Wheater, C. P., W. R. Cullen, and J. R. Bell. 2000. Spider communities as tools in monitoring reclaimed limestone quarry landforms. Landscape Ecology **15:**401–406.

White, P. S., and J. L. Walker. 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. Restoration Ecology **5:**338–349.

White, R. E. 1983. A field guide to the beetles of North America. Edited by R. T. Peterson. Vol. 29, The Peterson field guide series. Houghton Mifflin, Boston.

Williams, K. S. 1993. Use of terrestrial arthropods to evaluate restored riparian woodlands. Restoration Ecology **1:**107–116.