Chapter 3. Assessment of Unreplicated Restoration Attempts Using Terrestrial Arthropods

Introduction

Ecological restoration properly should have the goal of recreating the entirety of an ecosystem, including the invertebrate fauna (Longcore *et al.* 1999). The recovery of the invertebrate fauna on restored sites has been used to assess the performance of restorations (Andersen and Sparling 1997; Greenslade and Majer 1993; Jansen 1997; Parmenter and MacMahon 1990; Peters 1997; Williams 1993). Such attempts, however, depend on the ability to compare the site to reference conditions adjacent to or near the site if the previous condition of the site being restored is unknown (White and Walker 1997).

Reference sites are used to describe the conditions — species composition, abundance, diversity — of the natural habitat that is the goal of a restoration project. Comparison with such conditions allows an evaluation of the progress of the restoration. The site for the measurement of these conditions is usually not the restoration site itself, as it is presumably already degraded unless surveys prior to degradation were made for some reason. Rather, it is most often a nearby undisturbed habitat. The reference site may be measured simultaneously with the restoration with which it is to be compared, or measurements may be taken and established during previous years. For the purpose of defining reference conditions for arthropods, the high yearly variation in abundance exhibited by this phylum in areas of Mediterranean climate recommends where possible that comparisons of arthropod communities at restorations and reference sites be conducted with data collected during the same period, under the same climatic conditions. Alternatively, a long-term dataset (30 years) could be used because it would incorporate the full range of climatic variation. Few such datasets exist but shorter datasets collected at reference sites during previous years can be used to define a range of variation exhibited by arthropod communities (Samways 1990b; Wolda 1992) and to identify species that may be good indicators because their responses to habitat conditions transcend yearly variation.

While establishing reference conditions for restorations is attractive in that thay provide a goal for the restorationist to achieve, they generally fail to provide for assessment of alternative outcomes of the restoration project. That is, reference conditions provide a definition of the ideal outcome of restoring a community untouched by anthropogenic disturbance. Equally useful for purposes of evaluating restorations is to describe a range of conditions with which to compare the restoration. For example, a restored habitat may be similar to a native habitat that has been undergoing succession without interference. For this reason, I used the concept of "comparison sites" that exhibit a set of different conditions with which to compare the restoration. This differs from the usual definition of reference conditions, which does not include disturbed habitats.

In the previous chapter, I used the results of a five-year monitoring effort to describe the composition of pitfall-trapped arthropods in coastal sage scrub and their interannual and seasonal variation. The goal of this chapter is to develop quantitative methods to compare unreplicated restorations based on the results of arthropod monitoring with pitfall traps.

This goal also requires investigation of the relationship between vegetation characteristics and arthropods. The structure of arthropod communities at restored sites may be influenced by a number of ecological factors. Studies of old field succession have shown a positive relationship between plant species and structural diversity and arthropod diversity (Murdoch *et al.* 1972; Southwood *et al.* 1979; Hawkins and Cross 1982; Stinson and Brown 1983; Parmenter and MacMahon 1987; Parmenter and MacMahon 1990). As far as arthropod guild structure is concerned, a good indicator of a successful restoration should be rare, predatory arthropods (Peters 1997). Because other studies of guild structure during succession use more comprehensive sampling measures (*e.g.*, sweep netting, vacuuming) than the present study (pitfall trapping), the guild proportions shown in those studies (Teraguchi *et al.* 1977; Moran and Southwood 1982; Hendrix *et al.* 1988) are not likely to be replicated by pitfall trapping.

Exotic arthropods will also likely be an indicator of restoration success or failure. Argentine ants have received the most attention as invaders in Mediterranean ecosystems (Erickson 1971; Ward 1987; Cole *et al.* 1992; Holway 1995; Human and Gordon 1996; Human and Gordon 1997; Suarez *et al.* 1997; Way *et al.* 1997; Holway 1998a; Holway 1998b; Holway *et al.* 1998; Human *et al.* 1998; Kennedy 1998; Suarez *et al.* 1998; Holway 1999), but several other species (*Armadillidium vulgare*, *Porcellio laevis*, *Forficula auricularia*, and *Dysdera crocata*) are likely also important (Paris and Pitelka 1962; Paris 1963; Langston and Powell 1975; Barthell *et al.* 1998; Bolger *et al.* in press).

Based on this literature, the null hypotheses to be addressed in this chapter are:

- Restored and comparison sites have identical terrestrial arthropod communities, as measured by composition, abundance, and richness.
- Restored and comparison sites exhibit similar abundance and species richness of exotic arthropods.
- Terrestrial arthropod community structure in restored and comparison sites is not explained by plant taxonomic or structural diversity.
- Exotic species have no effect on overall arthropod species diversity.

Monitoring sites in the present study 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.

Methods

Study Localities and Sites

The coastal sage scrub localities studied are described in Chapter 2. The comparison localities are those described as “disturbed” and “undisturbed”. The undisturbed comparison localities provide “reference” conditions *sensu* White and Walker (1997). They are: Kelvin Canyon, Klondike Canyon, Portuguese Canyon, Inspiration Point, DFSP-Disaster Shelter, DFSP-Office, and DFSP-Locoweed. The disturbed comparison localities are Malaga Canyon, Fennel Hill, DFSP-South End, and DFSP-Hill. The restoration localities are described in more detail here. Each locality was sampled at 2–3 trapping “sites” separated by 20 m as topography and vegetation allow; “sites” are the locations of individual traps, whereas “localities” are clusters of 2–3 trapping “sites.”

Crystal Cove and Pelican Point. Two localities in the Crystal Cove State Park were included in the study: Pelican Point and Crystal Cove. In the design of the study, I originally assumed that the Crystal Cove locality was an undisturbed reference. However, the first several months of arthropod data showed it to be rather impoverished, and subsequent investigation confirmed that it too was a restoration site. Both sites are on a coastal bluff in an area with a history of agricultural exploitation, and it is likely that both sites were dry farmed. They are however, contiguous with the bluff face, which has never been substantially disturbed and should have provided a refuge for the terrestrial arthropod community. According to records provided by park staff, Pelican Point was both seeded and planted in 1984 and Crystal Cove was seeded in 1985. However, plants with nursery tags are also found on the Crystal Cove site, suggesting that it too had been planted. The revegetation effort at the Park has been documented (Hillyard 1990).

Ocean Trails. The Ocean Trails West Bluff preserve was revegetated as compensatory mitigation for the construction of a golf course on a coastal bluff. The 4.5-acre site is adjacent to undisturbed bluff face. The site had been used for agriculture through the first half of the century and had lain fallow with some reestablishment of native shrubs for at least 30 years prior to revegetation. The locality was heavily covered with invasive exotic plant species, including fennel (*Foeniculum vulgare*) and mustard (*Hirschfeldia* sp.). The revegetation protocol included mowing followed by disking and seeding, then another round of disking and seeding and the final planting of container stock. Final planting was completed in the fall 1994.

DFSP-Restoration. This locality is part of an ongoing revegetation effort focused on providing habitat for the federally endangered Palos Verdes blue butterfly (Mattoni 1994; Isbell 1996; Gross 1997). Because of its location on a military installation for the last 50 years, it has not been actively used for agriculture, although land use prior to the construction of the installation is unknown. It was likely disturbed in the last ten years by the construction of a small runoff channel through the site. During 1997 the site was cleared of exotic species (mostly Mediterranean grasses) by hand and planted with native shrub species. Although irrigated during shrub establishment during the fall of 1997, it was not irrigated during the study period.

Sampling Methodology

Pitfall Trapping. The trapping methodology and trapping success is described in the previous chapter. Data 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, including Fisher's alpha, which was chosen as the appropriate measure based on the observed species abundance pattern. Because the sampling for the restorations at Crystal Cove State Park (Crystal Cove and Pelican Point) was started three months later than the other restorations, only nine months of samples (April through December) were used for analyses that compared sites at the restoration localities with sites at comparison localities. Sites with more than one unsuccessful trap month were excluded from analyses involving comparisons of restorations with reference sites. This was necessary because of the observed seasonal variation in arthropod abundance established in the previous chapter. Use of data from other years or different numbers of successful samples would not provide an accurate comparison of the diversity at each site. However, the use of the shorter time span for analysis does decrease the ability to discriminate patterns. Some relationships that have shown to be significant using more samples are still evident but with less statistical certainty with the use of fewer samples. Analysis that involved only the comparison sites used twelve months of data.

Each species was assigned to a guild based on available reference materials (Borror and 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 traps (sites) at each locality were measured 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 touches of each plant species in each of the 10 height classes was recorded. For the remaining 20 locations all species touched by the pin were recorded. From these data, a plant spatial diversity was quantified using the technique described by Hendrix *et al.* (1988). The height index is used as a measure of structural complexity (Gibson *et al.* 1987; Hendrix *et al.* 1988):

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

where h = the midpoint of each height class i, n = the number of touches at height class i, and N = number of height classes represented by the sample (Hendrix *et al.*

1988). Plant species touches from all 30 locations were used to calculate native species richness, Shannon-Wiener diversity, and the percent native cover.

Statistical Techniques

Analysis of Variance. Differences in arthropod and vegetation parameters between sites were compared using analysis of variance in which reference and disturbed sites (*sensu* White and Walker 1997) were each treated as one group and compared to each of the restoration sites separately. All pairs compared using the Tukey-Kramer Honest Significant Difference (HSD) 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 parameters compared were diversity (Shannon-Wiener), number of touches, height index, number of native species, and percent native cover.

Multiple Regression. Relationships between vegetation and arthropod parameters 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 touches) were used to create models for arthropod diversity (Fisher's alpha), number of species, and number of individuals. Models were created for reference 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.

Cluster Analysis. Ward's method of agglomerative clustering was used to produce dendrograms based on the abundance of arthropod species. Similar site level analyses were conducted based on plant species abundance and vegetation structure using number of touches per height class as input data.

Correspondence Analysis. All specimen numbers for the period with complete sampling, April–December 1998, were log transformed to normalize their distribution (Figure 19). Sites and arthropod species were ordinated using detrended correspondence analysis (ter Braak 1987–1992; ter Braak and Prentice 1988; ter Braak 1996). 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 environmental variation was suggested in the previous chapter, so the assumption of a normal response curve to spatial variation is supported. The localities are assigned scores and can then be plotted on two axes.

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 successful collections averaged 45.99±40.38 S.D. specimens of 9.11±3.65 S.D. species. The distribution of specimens per collection was not normal because of large specimen counts in some collections (Figure 18). Log transformation normalized the number of specimens per collection (Figure 19).

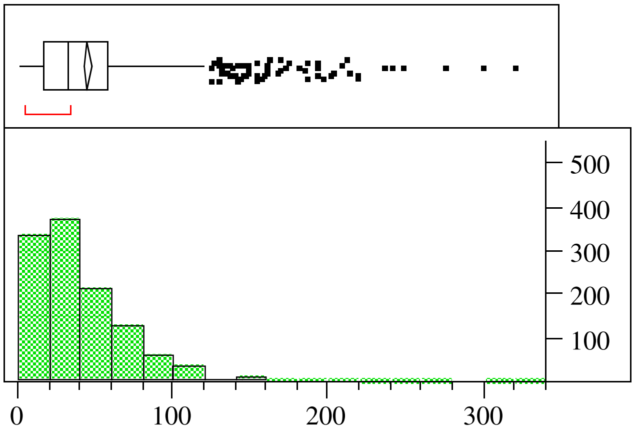

Figure 18. Distribution of arthropod specimens per collection. The x-axis reports the number of specimens per collection and the y-axis is the number of collections with this number of specimens. Each collection is one month trapping at one site. Above the graph is an outlier box plot. The ends of the box are the 25th and 75th quantiles of the data. The vertical line across the box is the median sample value. The diamond within the box is around the sample average. The lines extending from the box, called "whiskers," indicate 1.5 times the interquartile distance. The bracket to the left below the box identifies the densest 50% of the observations. Squares beyond the whiskers indicate outlier values. These graphical representations aid in making the determination that the sample distribution is not normal.

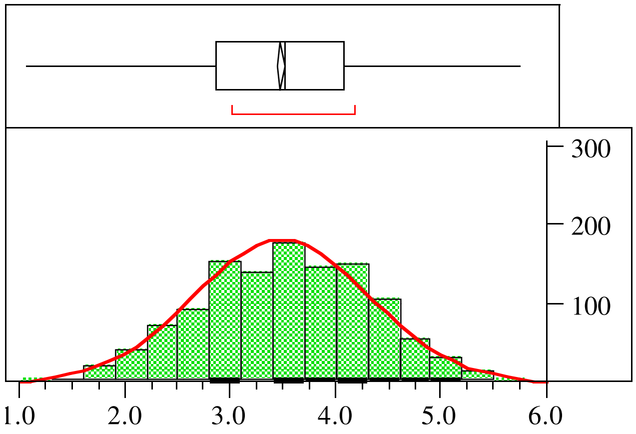

Figure 19. Distribution of log transformed arthropod specimens per collection. The x-axis reports the log transformed number of specimens per collection and the y-axis is the number of collections with this number of specimens. The lack of outliers, the confluence of mean and median, and the correspondence of the densest 50% of observations with the middle quartiles indicate a normal distribution.

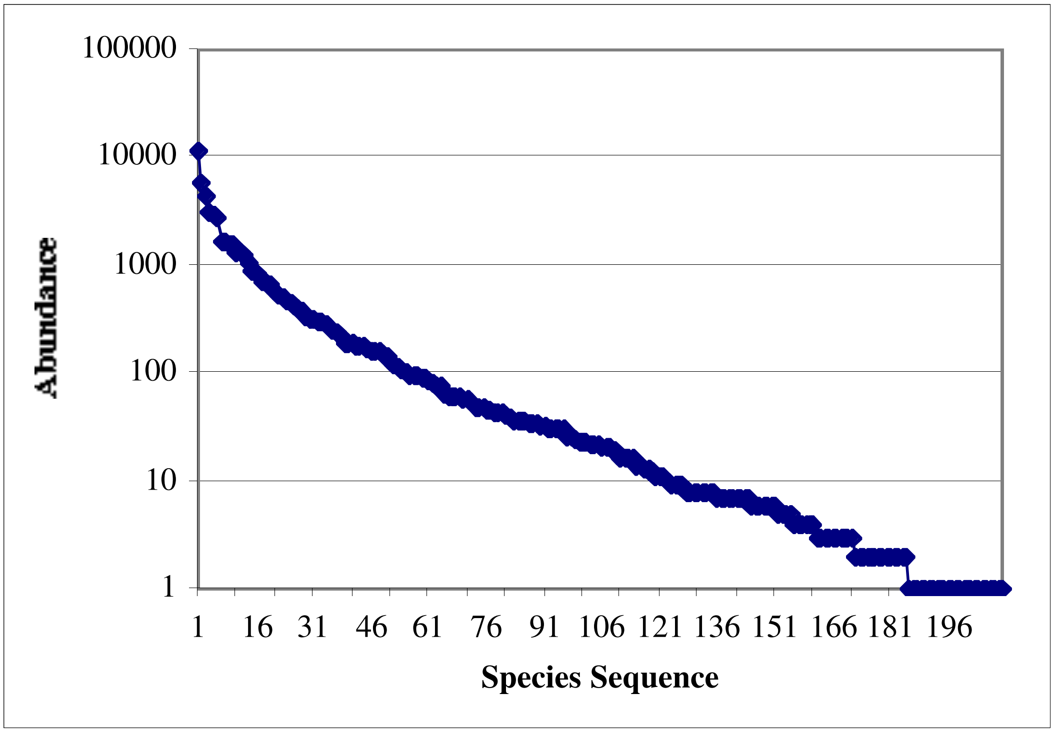

Figure 20. Number of individuals per species (rank abundance curve) for all collections, 1994–1998. Species are arranged in decreasing abundance along the x-axis. Note that the y-axis is on a log-10 scale.

The rank species abundance curve for the entire collection indicates that the distribution of species follows a log normal distribution (Figure 20) (Magurran 1988). Individual site 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, as 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).

Table 5. Summary statistics for arthropod diversity and abundance by category (mean±S.E., standard error uses a pooled estimate of error variance).

	Number of sites	Fisher's alpha	Total Species Observed	Mean Specimens
Disturbed	7	9.56±1.27	34.14±5.27	43.13±22.19
Reference	19	9.49±1.49	32.93±5.47	38.02±17.64
DFSP-Restoration	3	8.75±1.39	42.00±6.08	124.77±27.69
Ocean Trails	3	7.16±0.88	26.00±2.00	31.34±5.14
Crystal Cove/ Pelican Point	4	5.75±0.61	29.00±3.92	105.46±38.29

Using Fisher's alpha as the appropriate measure of arthropod diversity, the diversity of arthropods at undisturbed reference sites was greater than the two older restoration sites, Ocean Trails ($p<0.1$) and Crystal Cove/Pelican Point ($p<0.05$) (Figure 21). The DFSP restoration was not significantly different. When twelve monthly samples were used for the Ocean Trails comparison, confidence increased ($p<0.05$). The differences in species number were insignificant, with DFSP-Restoration recording the maximum number of arthropod species and the other two restorations with the fewest (Figure 22). DFSP-Restoration and the combined Crystal Cove/Pelican Point restoration localities had significantly more individuals than all other sites (Table 5 and Figure 23).

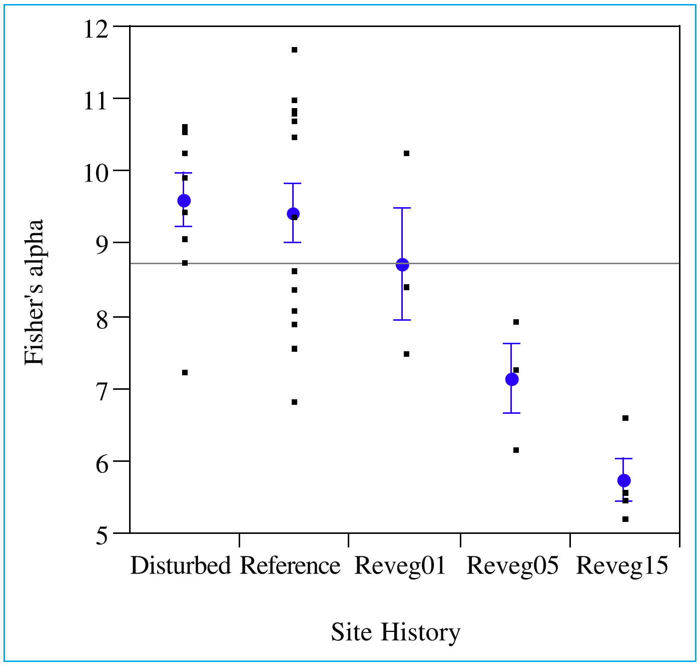

Figure 21. Arthropod diversity (Fisher's alpha) by site history. Restored sites are indicated by time since revegetation: Reveg01 = DFSP-Restoration, Reveg05 = Ocean Trails, Reveg15 = Crystal Cove and Pelican Point. Squares show values from each trap site, means with standard errors plotted.

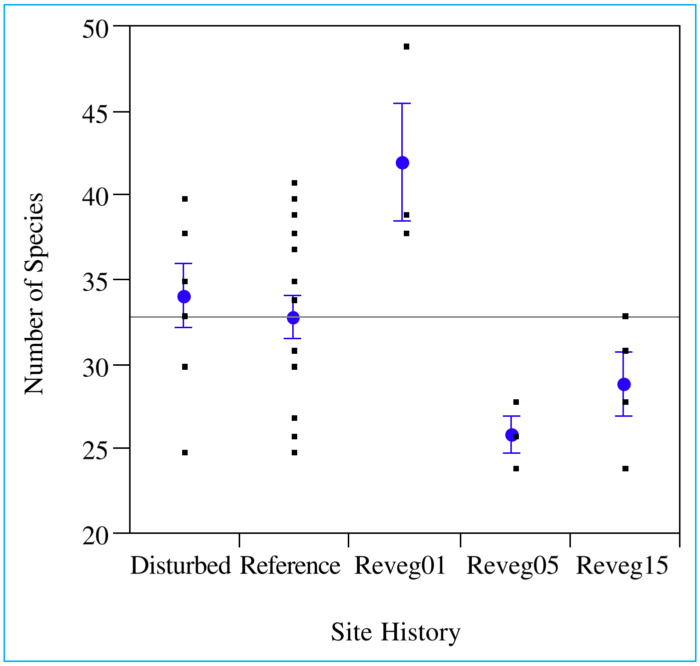

Figure 22. Total number of arthropod species sampled by site history. Legend same as Figure 10.

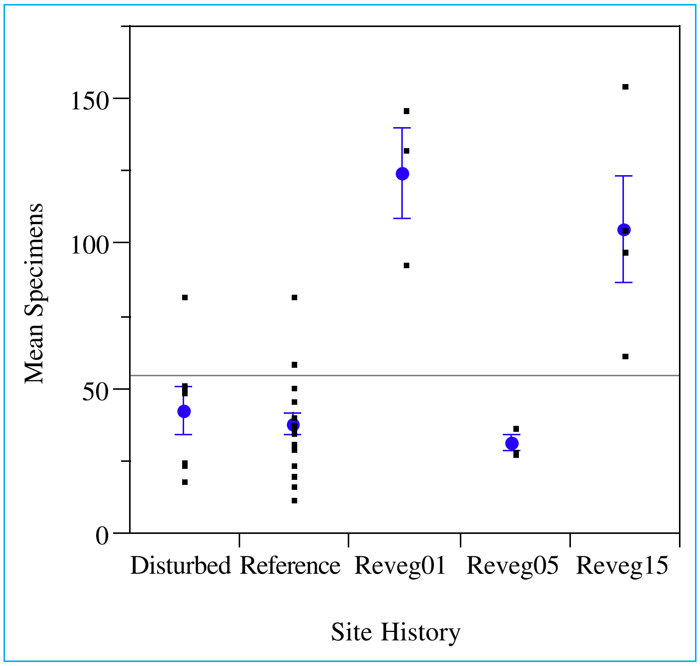

Figure 23. Mean number of arthropod specimens by site history. Legend same as Figure 10.

Vegetation Data

Results from vegetation sampling show few differences between disturbed, reference, and the restoration sites (Table 6). DFSP-Restoration was significantly more diverse than the reference sites, and it had significantly fewer plant touches than did any of the other categories. The disturbed sites had significantly fewer native plant species than did the reference sites, the Crystal Cover restorations, and DFSP-Restoration. DFSP-Restoration had a significantly lower height index than the reference sites, but not the other categories. The Crystal Cove restorations had a significantly larger percent native plant cover than disturbed sites or the other two restorations, while the reference sites had significantly larger percent native cover than disturbed sites and DFSP-Restoration.

Table 6. Summary vegetation statistics by site history (mean±S.E.). Superscripts indicate significantly different groups ($p<0.05$).

	Disturbed	Reference	DFSP-Restoration	Ocean Trails	Crystal Cove/Pelican Point
Number of sites	7	19	3	3	6
Shannon-Wiener dDiversity	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 touches	146.57 ± 23.81^{ab}	173.74 ± 9.14^{b}	75.333 ± 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}

Vegetation-Arthropod Relationships

Two vegetation factors significantly explained the number of arthropod species found at disturbed and reference sites combined: 1) a positive relationship with the number of native plant species ($p<0.004$) and 2) a negative relationship with vegetation height index ($p<0.004$) (model $r^2=0.48$) (Table 7).

The number of arthropod individuals had three predictors: 1) vegetation Shannon-Wiener diversity, 2) number of native plant species and 3) number of touches. The relationship is largely an artifact of the superabundance of a few species of exotic arthropods. These results were not explored further because of the large effect of exotic arthropods on total arthropod individuals. Arthropod diversity was predicted by: 1) the number of 40–60 cm height class touches ($p<0.002$), 2) vegetation height index ($p<0.0001$) and 3) percent native cover ($p<0.027$) (Table 8).

Table 7. Multiple regression results: explanation of arthropod species richness by vegetation parameters for reference and disturbed sites combined.

RSquare	0.48
RSquare Adj	0.43
Root Mean Square Error	3.61
Mean of Response	43.78
Observations	26

Parameter Estimates

Term	**Estimate**	**Std Error**	**t Ratio**	**Prob>|t|**
Intercept	47.24	2.96	15.96	<.0001
Number native plant species	1.12	0.35	3.19	0.0041
Vegetation height index	-0.17	0.05	-3.24	0.0036

Table 8. Multiple regression results: explanation of arthropod diversity (Fisher's alpha) by vegetation parameters for disturbed and reference sites combined.

RSquare	0.66
RSquare Adj	0.62
Root Mean Square Error	1.13
Mean of Response	11.96
Observations	26

Parameter Estimates

Term	**Estimate**	**Std Error**	**t Ratio**	**Prob>|t|**
Intercept	12.05	0.92	13.03	<.0001
Number of touches 40–60 cm	0.09	0.03	3.47	0.0022
Vegetation height index	-0.08	0.02	-4.88	<.0001
Percent native cover	2.06	0.87	2.37	0.0272

For reference and disturbed sites, the model for exotic species included one species, the European earwig (*Forficula auricularia*), which explained 29% of the variation in overall arthropod diversity (Table 9). The model including all sites showed significant predictive value for abundance of 1) Argentine ants (*Linepithema humile*), and 2) the Sowbug Killer (*Dysdera crocata*) with an overall model explanation of 48% (Table 10).

Table 9. Multiple regression results: explanation of arthropod diversity (Fisher's alpha) by exotic arthropod species for reference and disturbed sites.

Summary of Fit	
RSquare	0.29
RSquare Adj	0.26
Root Mean Square Error	1.57
Mean of Response	11.96
Observations	26

Parameter Estimates

Term	**Estimate**	**Std Error**	**t Ratio**	**Prob>|t|**
Intercept	13.13	0.49	26.97	<.0001
Forficula auricularia	-1.89	0.61	-3.10	0.0049

Table 10. Multiple regression results: explanation of arthropod diversity (Fisher's alpha) by exotic arthropod species for all sites.

Summary of Fit	
RSquare	0.48
RSquare Adj	0.44
Root Mean Square Error	1.36
Mean of Response	10.65
Observations	32

Parameter Estimates

Term	**Estimate**	**Std Error**	**t Ratio**	**Prob>|t|**
Intercept	10.73	0.46	23.25	<.0001
Dysdera crocata	-2.61	1.46	-1.79	0.0847
Linepithema humile	-1.03	0.31	-3.34	0.0023

Arthropod Guild Composition

The Argentine ant dominated the exotic species and guild structure (Table 11), ranging from 5.9–54.3% 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 ranged from 5.1–41.0%. 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 reference sites. The lower percentages of native guilds is 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 reference sites.

Table 11. Mean percentage of arthropods by guild and nativity. Guilds are ants (Ant), phytophages (Phyt), predators (Pred), parasites (Para), and scavengers (Scav).

Locality	Exotic Ant	Exotic Phyt	Exotic Pred	Exotic Scav	Total Exotic	Native Ant	Native Para	Native Phyt	Native Pred	Native Scav
Reference										
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 Trail	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%

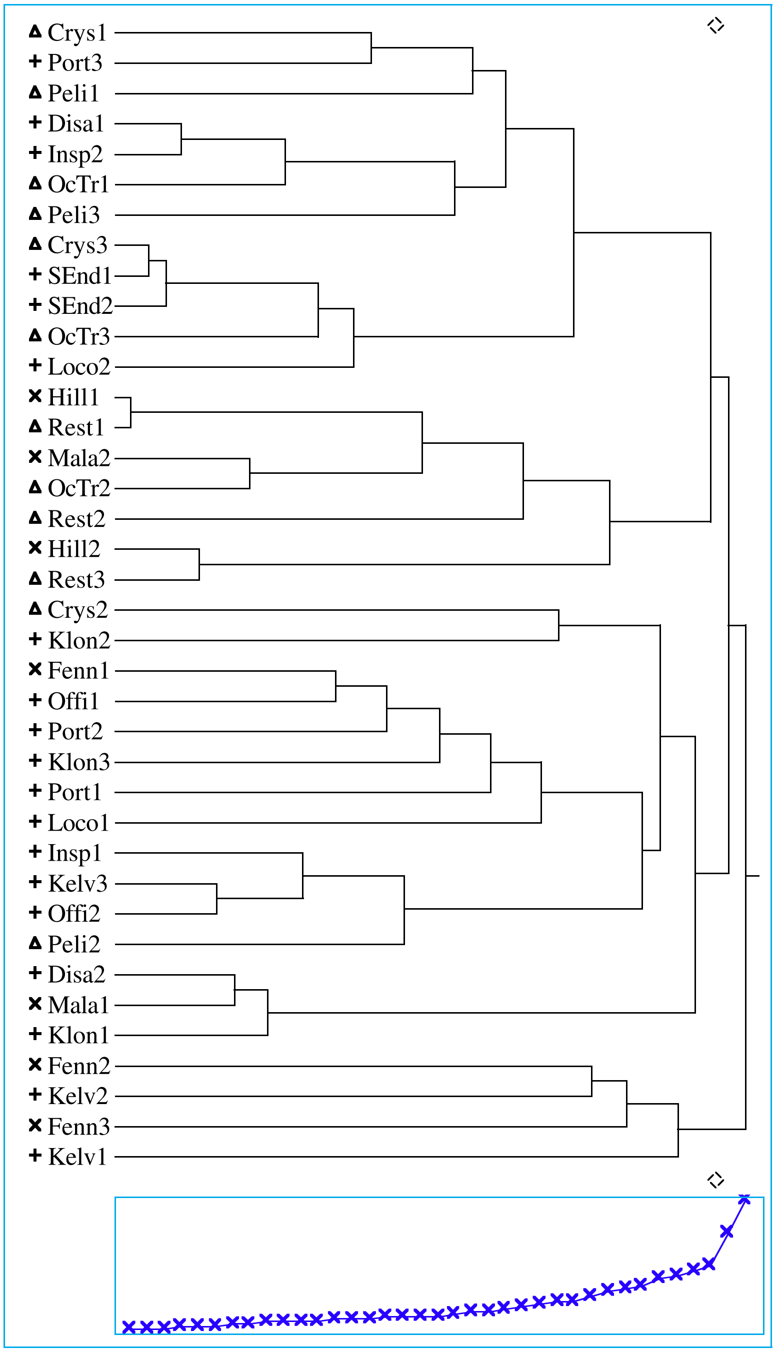

Figure 24. Cluster analysis of sites based on plant structure. Raw height class data used for Ward's method. Note that the clusters formed include restored, disturbed, and reference sites with each other. The plot beneath the dendrogram has a point for each cluster join. The ordinate is the distance that was bridged to join the clusters at each step. Symbols at left indicate reference (+), disturbed (X), and restoration sites (Δ).

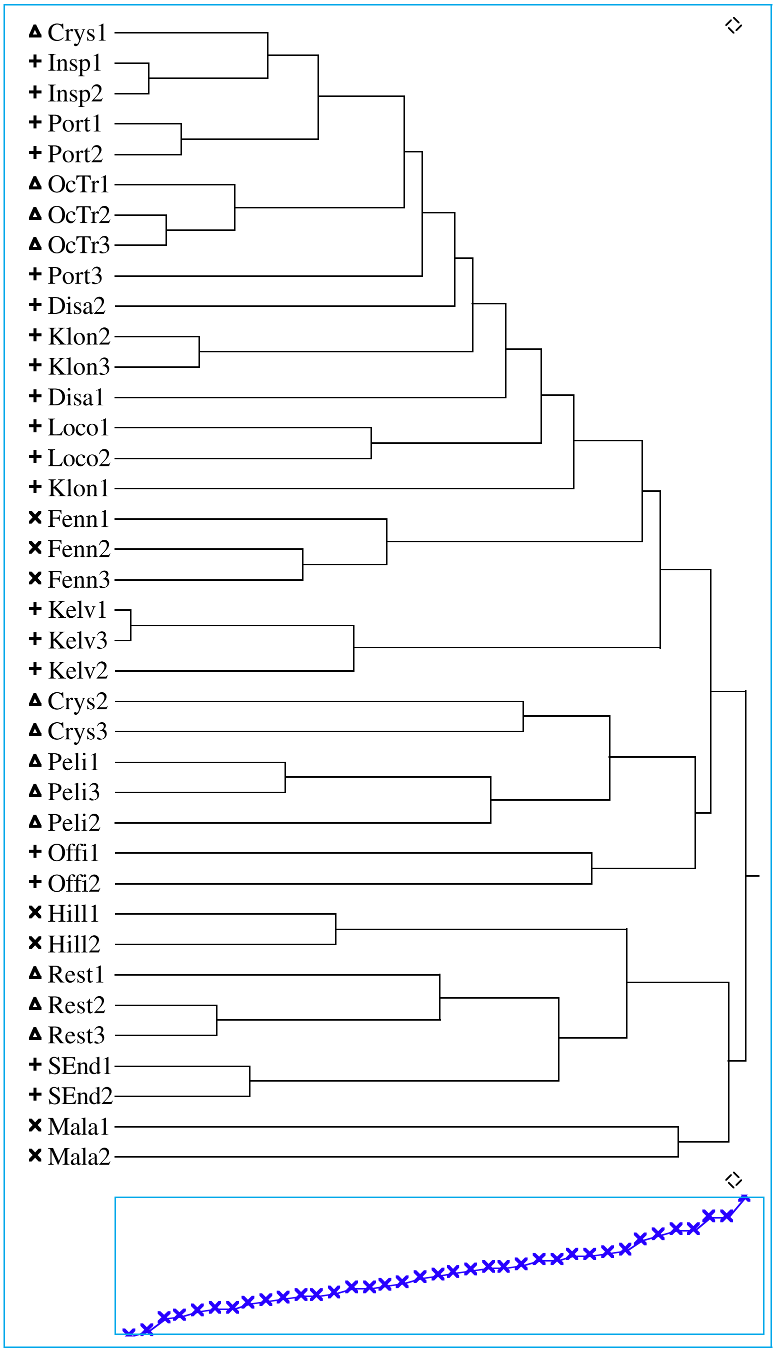

Figure 25. Cluster analysis of sites based on plant species data. Log transformed species abundance used for Ward's method. Note increased cohesion between sites at a locality when compared to structural diversity, but also clustering of restorations with reference and disturbed sites. Symbols at left indicate reference (+), disturbed (X), and restoration sites (Δ).

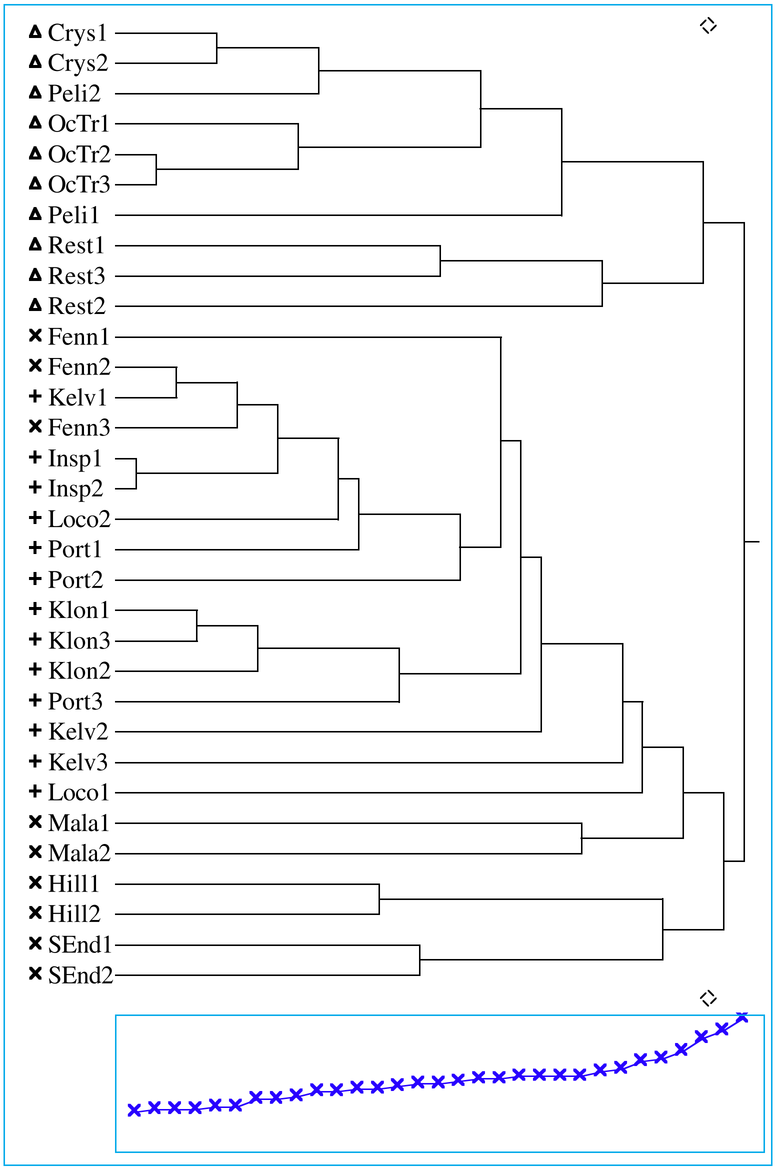

Figure 26. Cluster analysis of sites based on arthropod data. Sites with missing months are omitted as described above. Note that all restorations are separated from other sites at first division. Symbols at left indicate reference (+), disturbed (X), and restoration sites (Δ).

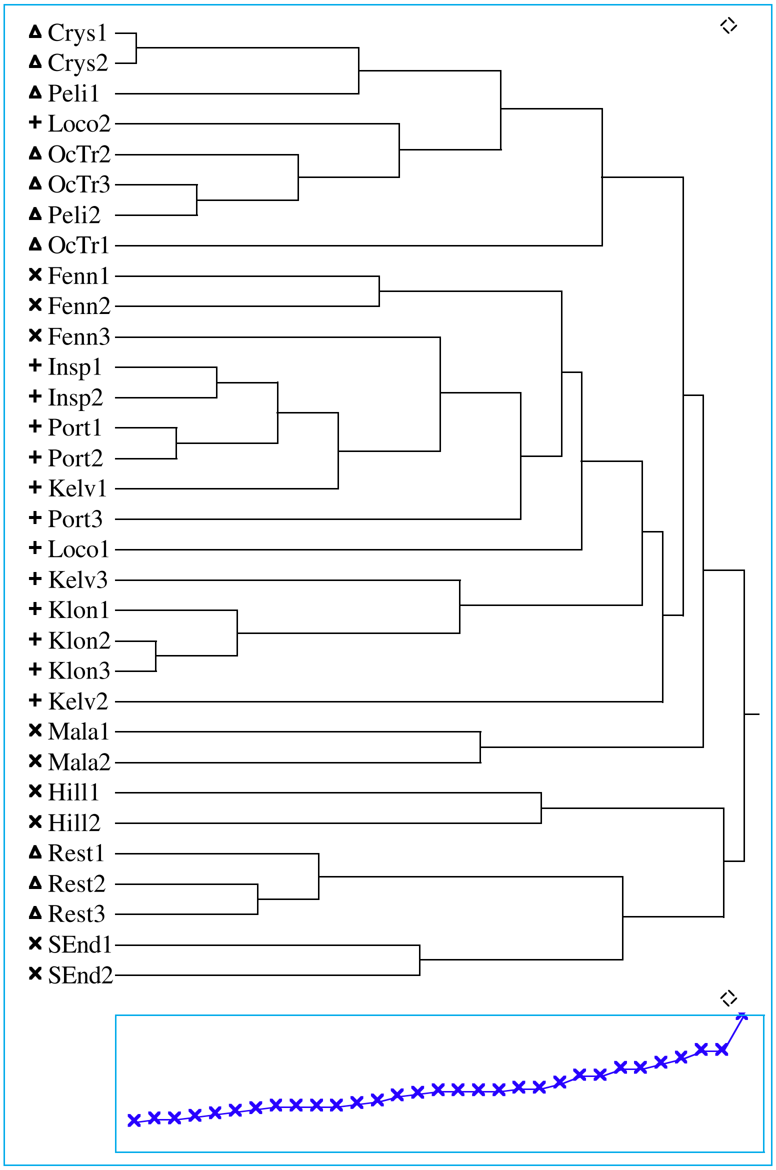

Figure 27. Cluster analysis of sites based on native arthropod abundance only. Symbols at left indicate reference (+), disturbed (X), and restoration sites (Δ).

Cluster Analysis

Cluster analysis of sites using vegetation height class data produced three distinct clusters of short, medium and tall vegetation (Figure 24). Sites from the same locality did not cluster together, and samples from restoration, disturbed, and reference sites clustered with each other and did not produce exclusive groups.

The dendrogram produced for plant species did show cohesion among samples from the same site; all terminal pairs contained samples from the same site and 8 of 15 sites formed exclusive clusters (Figure 25). DFSP-Restoration clustered with the disturbed sites at the first level, with the other restoration sites interspersed with the reference sites.

Cluster analysis of sample sites based on arthropod species forms three large clusters: 1) DFSP-Hill and DFSP-South End, 2) all three restorations, and 3) all other sites (Figure 26). Seven of 14 sets of replicates formed exclusive clusters and all terminal pairs but one were replicates from the same site. Of the disturbed sites, Fennel Hill clustered in with reference sites. The height of vegetation at Fennel Hill influences its arthropod community. As shown below, the 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. The two interesting differences were: 1) DFSP-Restoration sites clustered with the other disturbed sites at DFSP, rather than with the other restorations, 2) DFSP-Locoweed 2 clustered with the restorations at Crystal Cove.

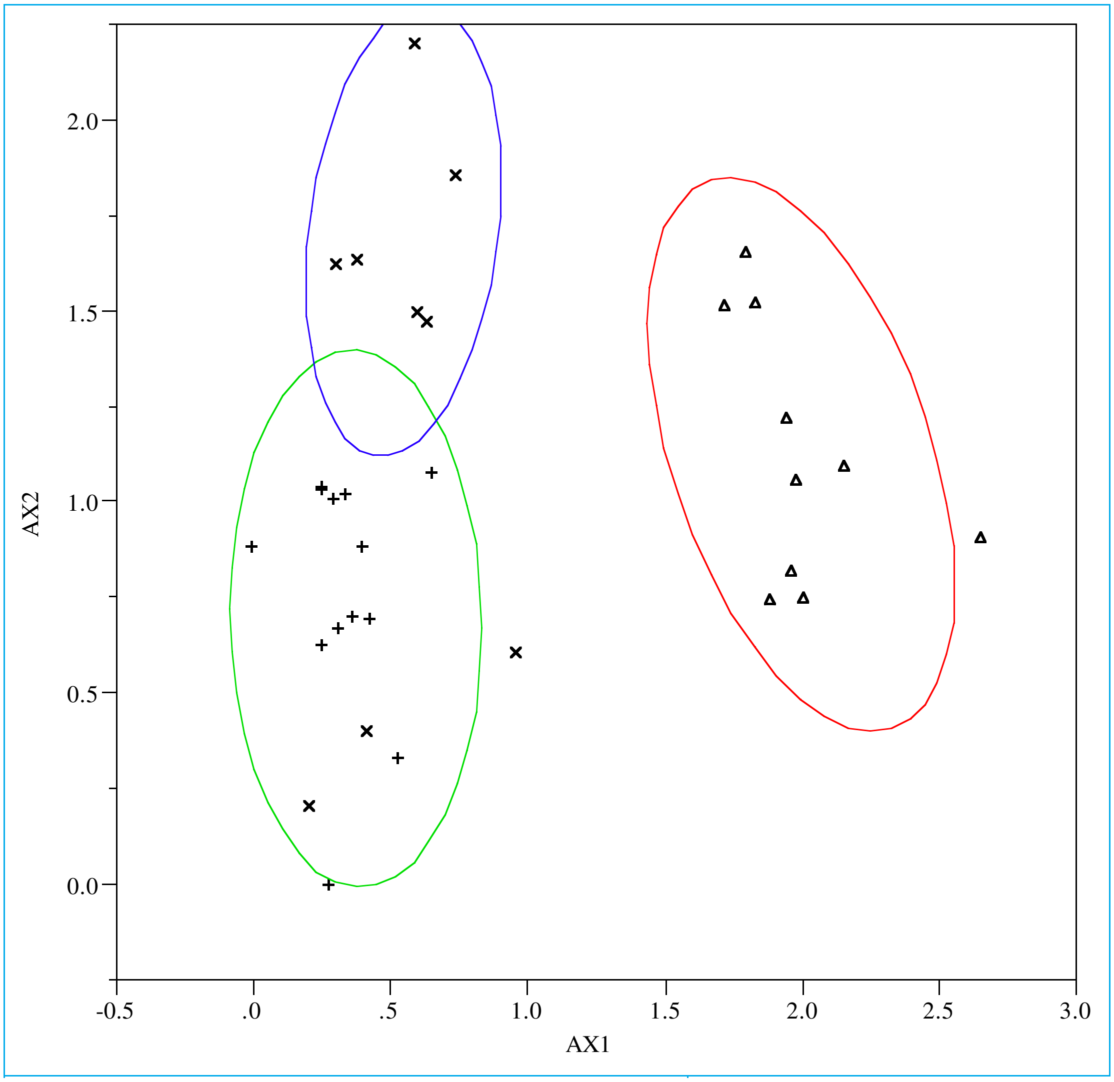

Figure 28. Detrended correspondence analysis of arthropod species and site data. Bivariate ellipses show clusters based on first two axes. Symbols indicate reference (+), disturbed (X), and restoration sites (Δ).

Detrended Correspondence Analysis

The log-transformed arthropod abundance data were used in detrended correspondence analysis. Detrended correspondence analysis (Table 12) separated restoration from reference and disturbed sites on the first axis (Figure 28). Restorations had significantly ($p<0.01$) higher scores on the first axis than reference and disturbed sites; and although not as pronounced, disturbed sites had significantly ($p<0.05$) higher scores than reference 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 most exotic species. The second axis separates early succession disturbed sites from other reference sites along a height gradient. The axis is significantly correlated with the height index of the vegetation ($r^2=0.54$, $p<0.0001$).

Table 12. Detrended correspondence analysis of arthropod communities.

Axes	1	2	3	4	Total inertia
Eigenvalues	.388	.190	.120	.083	2.866
Lengths of gradient	2.660	2.199	1.833	1.668	
Cumulative percent variance of species data	13.6	20.2	24.4	27.6	

Discussion

Of the three restoration sites sampled, none had developed an arthropod community that resembled that of undisturbed or disturbed native coastal sage scrub (Figure 28). 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 over time to a more natural structure. In fact, the oldest revegetation — Crystal Cove State Park — was dominated by exotic arthropods and exhibited extremely low arthropod diversity.

Vegetation parameters explained a substantial portion (48–66%) of the variation in arthropod communities in reference and disturbed sites. The one relationship found that is consistent with succession theory is that between arthropod diversity and vegetation height and complexity. Southwood *et al.* (1979) described increasing insect taxonomic diversity while plant taxonomic and spatial diversity increase, 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 with respect to succession over time. When including the disturbed sites on the continuum of height indexes documented in the study, there is an arch in arthropod species diversity with the height of vegetation. The subsequent model to describe arthropod diversity by site class data further illuminated this relationship with respect to terrestrial arthropods measured by pitfall trapping.

Increased plant touches (*i.e.*, greater complexity) at 40–60 cm above the ground is correlated with higher arthropod diversity, while complexity at greater heights (and a correspondingly greater height index) was correlated with lower arthropod diversity. This relationship is not spurious, because height index and touches at 40–60 cm are positively, not negatively, correlated. Southwood *et al.*'s (1979) other predictor, plant diversity, was not found to have a significant relationship, but rather percent native cover emerged as a significant predictor of overall arthropod diversity at native coastal sage scrub sites.

For restoration sites, the percent native cover or the number of native plant species was not correlated with increased arthropod species richness or diversity. To the contrary, because of the high native cover of the Crystal Cove restorations and their equally low arthropod diversity, the relationship was the opposite of that expected. Furthermore, all of the restoration sites supported plant communities similar in species incidence and abundance to comparison sites. Vegetation at the

DFSP restoration was similar to the early succession disturbed sites. However similar their vegetation to comparison sites, the restoration sites did not support similar arthropod communities. The cluster analysis and DCA strongly support this result as well.

The importance of exotic species in determining arthropod communities cannot be understated. However, this effect was not uniform among reference, disturbed, and restoration sites. For reference 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*, could explain 48% of the variance in overall arthropod diversity. First, this illustrates that the negative correlation between exotic species abundance and overall arthropod diversity is much stronger in 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 reference 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). By contrast, the relatively high native arthropod diversity at the 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.

Other measured variables cannot account for the distinctness of the arthropod communities at Ocean Trail and Crystal Cove. The effect of regional changes in species composition (beta diversity) was eliminated from the dataset by dropping species found at fewer than three localities from the analysis. Distance to source areas was eliminated as a variable because each restoration was adjacent to native habitat, coastal bluff scrub in the case of Ocean Trails and Crystal Cove/Pelican Point and remnant coastal sage scrub at DFSP. Results from these localities illustrate that creation of a native plant community does not necessarily result in the recreation of a native arthropod community. Site disturbance history, assembly rules, and restoration technique remain as probable explanations of their depauperate character.

In addition to the overall differences in arthropod diversity and exotic species abundance between native and restored sites, several species were found only at reference sites, and these may serve as indicator species. The likely candidates for indicator species are the charismatic megafauna of the arthropod world, viz., large predators such as scorpions. Indeed, of the scorpion species found during the study, the burrowing scorpion (*Anuroctonus phaiodactylus*) and common scorpion (*Vejovis* sp.) were limited entirely to reference sites at Kelvin, Klondike, and Portuguese canyons. Stripe-tailed scorpions (*Paruroctonus silvestrii*) were predominantly found at reference sites but were also found in small numbers at each of the restorations. Another unique predator, the trap door spider (*Aposticus* sp.), was found almost exclusively at reference sites, but with a few records from the restoration at Pelican

Point. For other predators, no psuedoscorpions or assassin bugs were found at restoration sites but were found at reference sites. In addition, although not a predator, the sand roach (*Arenivaga* sp.) was found almost exclusively at reference 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% 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 and McCormick 1986; Polis *et al.* 1989; Holt and Polis 1997). In experimental manipulations, removal of scorpions resulted in a doubling in spider number (Polis and 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.* (in press). Lack of population regulation by scorpions is a complementary hypothesis to their suggestion that a more productive detrital food web explains high spider abundance in old, isolated fragments (Bolger *et al.*, in press).

Summary

The results support the overall objective of assessing restoration sites undertaken at different times with different methodologies using terrestrial arthropods. The arthropod species are distributed normally and exhibit sufficient variation to be used as metrics to evaluate restoration projects. In this respect, the study joins a number of other studies using arthropods to evaluate restoration projects. The clustering of replicate traps together in cluster analysis also reinforces the adequacy of the experimental design. Restoration sites had lower arthropod diversity than undisturbed reference sites. This difference was also evident in cluster analysis based on those data and could not be attributed to differences in vegetation at the sites. Detrended correspondence analysis also separated restoration sites from all others. The differences between restoration sites and their natural analogues were closely related to higher abundance of exotic arthropods at restoration sites. Rare predatory species are absent or present in significantly lower abundance at restoration sites.

Chapter 4. Terrestrial Arthropods and Restoration: If You Build It, Will They Come?

Introduction

Ecological restoration has become an increasingly common tool in land management and conservation planning. While some projects have been designed to provide habitat for butterflies (Mattoni 1988; Mattoni 1989; Marttila *et al.* 1997; Longcore *et al.* 1999), insects and arthropods as a whole have not been the target of restoration attempts. Although not target organisms, terrestrial arthropods have been used as indicator species to assess restoration attempts for 30 years (Hawkins and Cross 1982; Parmenter and MacMahon 1987; Parmenter and MacMahon 1990; Parmenter *et al.* 1991; Williams 1993; Andersen and Sparling 1997; Williams 1997). The study of insect communities in old fields undergoing succession has provided understanding of the response of insects to changing plant communities, which the maturation of revegetation plantings theoretically emulates (Southwood *et al.* 1979; Brown and Southwood 1983; Brown and Hyman 1986; Hendrix *et al.* 1988; Brown 1991; Edwards-Jones and Brown 1993; Hollier *et al.* 1994). The research presented in the preceding chapters adds to the understanding of both the response of arthropods to restorations and the use of arthropods as indicators of restoration progress. The importance of those results, their relationship to previous work, and their implications for restoration methodology are discussed in this chapter.

Five major themes emerge as important areas of discussion vis-à-vis arthropods and restoration. First is the validity of the “Field of Dreams” approach to restoration that holds, “If you build it, they will come.” In this way of thinking, it is sufficient for restoration projects to revegetate with native plants. It is assumed that once a native plant community is in place, the native fauna —insects, reptiles, birds, and mammals — will colonize the site. Unfortunately, the available data only support this assumption in a few situations.

Second, the presence and abundance of invasive arthropods has a profound effect on the composition of arthropod communities on restoration sites. While the effect of invasive arthropods on habitat fragments has received considerable attention, their role in confounding restoration attempts has been largely unexplored. A potential explanation for the failure of native arthropods to recover in restorations can be found in community assembly rules, which suggest that the order of invasion of species has an effect on the final species composition.

Third, just as large mammalian predators are indicators of habitat quality at larger spatial scales, high quality habitats at smaller scales are associated with large, long-lived, predaceous arthropod species such as scorpions. These charismatic megafauna of the arthropod world can serve as indicators of restoration success. The lack of top predators in new restorations is consistent with sites in early succession, but an ongoing failure to support top arthropod predators at 15 years after restoration may indicate a chronic problem.

Fourth, arthropod species exhibit high yearly and seasonal variation in number that can be trapped. Such variation has implications for trapping methodology to assess restoration progress. Different responses of native and exotic species to climatic variables may also facilitate the successful invasion of exotic species.

Fifth, terrestrial arthropods respond positively to vegetation diversity in undisturbed habitats and in sites in succession. Failure of restorations to exhibit similar responses may indicate a larger problem with the recovery of the community. In the instances investigated in this study, the preponderance of exotic species overwhelmed any potential response of the native arthropod community to plant diversity.

The Field of Dreams Myth

In W. P. Kinsella's lyrical novel *Shoeless Joe* — later made into the popular movie *Field of Dreams* — the protagonist hears a voice telling him, "If you build it, he will come" (Kinsella 1982). While this admonition was directed to the construction of a baseball diamond in an Iowa cornfield for Shoeless Joe Jackson and the ghosts of the disgraced "Black Sox," its attractively simple approach seems to pervade most ecological restoration projects. The overwhelming attitude of regulators and restorationists has been that if the right plants are planted and survive, the other components of the native community will follow. This may be true for some components of the invertebrate community, but for terrestrial arthropods this sort of wishful thinking has not been borne out by the evidence.

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 and MacMahon 1987; Parmenter and MacMahon 1990; Parmenter *et al.* 1991).

Parmenter and MacMahon conclude that the severity of disturbance from mining may preclude forever development of a similar flora and fauna on the site (Parmenter and MacMahon 1987). Williams measured arthropods at restored and reference riparian willow forests using pan traps and sweep nets. Her measurements indicated that the restorations supported fewer individuals overall, as well as fewer predators and parasites (Williams 1993). In a study of carabid beetles in restored wildflower meadows, Blake found that after five years arthropods from restored sites were characterized by fewer species, lower diversity, and smaller body sizes than reference sites (Blake *et al.* 1996). 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 and Majer 1999). Finally, this study showed diversity and richness of arthropods in coastal sage scrub restorations 5 and 15 years old to be lower than reference sites.

When considering the success of restoration projects, aquatic and terrestrial arthropods seem to respond in distinctly different ways. While problems certainly abound with wetland restoration projects (Allen and Feddema 1996; Race and Fonseca 1996; Sudol 1996; Zedler 1996), success in recreating invertebrate communities, or at least the failure to detect differences from reference conditions, has been documented in aquatic habitats (Lingdell and Engblom 1995; Streever *et al.* 1996). Colonization and spread of species may be more easily accomplished through water than across land, which might explain the different results between terrestrial arthropods and aquatic or volant species.

Many scientists and restorationists do not immediately understand the importance of arthropods to the success of a restoration project. One reviewer for a grant proposal for this project expressed the opinion that plants were sufficient for “reclamation” projects. To the contrary, there are many reasons that scientists, restorationists, and regulators should be concerned that insects do not follow the Field of Dreams pathway to recovery.

For compensatory mitigation, the regulatory intent of restoration is to replace habitat damaged through permitted activities. Invertebrates, especially arthropods, constitute a significant portion of the biodiversity of terrestrial habitats. If restored sites are considerably less diverse, compensatory mitigation has not replaced the habitats that were destroyed in exchange for their creation.

Beyond the value of arthropods as entities themselves worthy of concern, they are critical to ecosystem function. E. O. Wilson has referred to invertebrates as “the little things that run the world” (Wilson 1987). Invertebrates are critically important as scavengers, converting decomposing materials into simpler forms more readily available to plants (Borror *et al.* 1989), they aerate soil and add to its organic content (Borror *et al.* 1989), and they are primary consumers of fungi, releasing important nutrients to the soil and facilitating plant-fungi associations (Hanlon and Anderson 1979). Insects are important food sources for small mammals, reptiles, and birds. Restorations with depauperate or abnormal insect communities will provide less forage for the bird species that are often targets of restoration attempts. Williams suggested that the smaller prey size of insects in restored riparian woodland was one reason that the restored site was foraged less by the target species, Least Bell’s Vireo, an insectivorous bird (Williams 1993). Other researchers have connected the lack of invertebrates in certain managed or restored landscapes to decreased bird abundance (Larochelle 1980; Blake *et al.* 1994; Pettersson *et al.* 1995; Blake *et al.* 1996; Pettersson 1996). Changes in insect community composition have also been demonstrated to harm vertebrate predators. The replacement of native ants by invasive ants in southern California canyons has resulted in the extirpation of Coastal Horned Lizards in many locations. The lizards will only eat the much larger native ants and disappear once the smaller exotic Argentine ants replace the native ants (Suarez and Case 1996; Suarez *et al.* 1997).

The importance of diversity in ecosystem functioning should not be underestimated. Some community attributes such as productivity have been shown to be more stable in diverse systems than less diverse counterparts, although the population stability of individual species may be lower (Putnam 1994; Tilman 1999). Walker has termed the existence of many species that serve similar ecological roles "ecological redundance" (Walker 1992; Lawton and Brown 1996). "Redundance" does not mean "unnecessary," but instead illustrates the importance of similar species being able to compensate functionally when another species population has declined (Walker 1995). Ecosystems and restoration projects that do not have ecological redundance as characterized historic conditions are more susceptible to collapse.

The available evidence does not support the notion of spontaneous recolonization of created habitats by arthropod communities similar to those in reference areas. A number of explanations for this phenomenon are possible and are discussed below. Moreover, such results should concern restorationists, because they mean that we have much more to learn about how natural systems work, how they are maintained, and how they develop. Thus far, we have failed the "acid test for ecology," to understand ecological systems sufficiently well to be able to recreate them (Bradshaw 1987).

Because invertebrates are crucially important to ecosystem function and restoration projects to date have not produced evidence of the development on restorations of communities similar to native habitats, regulators and restorationists could benefit from including invertebrates in restoration monitoring schemes and in performance standards.

Exotics and Community Assembly Rules

The second important theme emerging from a consideration of the results of this research and the ecological literature is the importance of invasive exotic species in influencing arthropod communities at restoration sites. While studies of biological invasions certainly provide evidence that exotic species can have profound effects on ecosystem properties (Orians 1986; Vitousek 1986; Vitousek 1990), and disturbance ecology reinforces the importance of the historical context for current landscape patterns (Sousa 1984; Pickett and White 1985), a further body of literature can help explain the patterns of exotic species abundance across restored and reference sites in this study. All of the study sites in this project were inhabited by exotic arthropod species. Even the least disturbed reference sites showed the presence of Argentine ants, European earwigs, and dooryard sowbugs, albeit at lower densities than restoration sites. The differences between reference and restoration sites were not attributable to vegetation characteristics. There were reference and restoration sites with very similar plant cover, but highly divergent arthropod communities. Assuming that the different sites had similar species pools that could invade, it is consistent with the observations that invasion history has a profound effect on community composition of restoration sites.

Numerous studies, including computer simulations, controlled laboratory experiments, and field observations, have shown that multiple stable communities may persist with any given species pool and that the order and rate of species invasion results in different stable communities (Sutherland 1974; Gilpin and Case 1976; Cole 1983; Gilpin *et al.* 1986; Robinson and Dickerson 1987; Robinson and Edgemon 1988). For experimental species assemblages, those species that were introduced first and at high densities were more likely to persist as dominant in the community (Robinson and Dickerson 1987).

Recognition of the influence of arrival order resulted in the development of community "assembly rules" (Diamond 1975). The argument is that the presence of some species preempts invasion by others, so that multiple combinations are possible based on the order of invasion. Gilpin (1987) highlighted the importance of this phenomenon to restorationists over a decade ago, but it does not seem that those in the rather messy business of implementing restoration projects have taken his challenging advice to "identify the crucial ("keystone") species and to introduce them in the correct sequence" (Gilpin 1987). Research on this topic has not been forthcoming since Gilpin's (1987) suggestion, mostly because there are no *a priori* characteristics that identify "keystone species."

I propose that for arthropod communities, the overlap between the ecology of invasive exotic species and patterns of community assembly make the order of species introduction important. All restoration sites are by definition disturbed, which provides conditions that promote invasion by exotic species through decreased habitat complexity (Petren and Case 1998), reduction in existing species number (Tilman 1997; Tilman 1999), disrupted physical parameters (Orians 1986), and proximity to human-influenced environments that provide colonists.

In southern California, nearly all degraded lands are occupied by invasive exotic arthropods. The restoration process may then provide more disturbance and unnatural conditions through grading, disking for weed control, application of herbicides, and other common management techniques. These actions do nothing to decrease the abundance of human-adapted invasive species but further degrade the remnant native arthropod community. The starting point for arthropod community recovery is rarely a clean slate, but usually a community already dominated by exotic, disturbance-tolerant species. The effect of invasion order provides one facet of an explanation for the differential degree to which invasive species, such as Argentine ants, dominate the fauna. Where the ants were given a head start through disturbance, and even the restoration process itself, they become a much more significant part of the arthropod community, even when a native plant community has developed.

Further research is necessary to confirm that the low diversity of some restoration sites resulted from the resistance to invasion by an established exotic species assemblage or from differences in habitat characteristics and other factors not detected by this study. However, even accepting it as a possible explanation can result in what should be rather practical recommendations for restoration practice.

Restoration attempts should make every effort to identify and protect the existing native arthropod community. Remnant native plants in a habitat should not be disturbed. Disking and other large-scale mechanical disturbance should be avoided — possibly including mechanized planting techniques such as seed imprinting, although more research is certainly needed to substantiate such a recommendation — save for instances where no native biological representation remains on the restoration site. This approach, one of doing no harm, requires trained hand labor and is much more labor intensive than more mechanized approaches. Implementation of such recommendations would certainly increase the cost of restoration projects, and would not find support among developers who must fund compensatory mitigation restoration projects to obtain their development permits.

Charismatic Megafauna, Guilds, and Indicators

The identification of indicator species for the assessment of terrestrial arthropod communities would be useful to regulators and implementers of restoration projects. Two types of indicators are possible, those whose *presence* can be taken as a proxy measure of the state of the arthropod community, and those for which *abundance* serves as the measure. Because of the variation in yearly abundance exhibited by these communities (Chapter 2), any measure depending on abundance would require simultaneous paired trapping at reference and restoration sites. For this method, the best indicators of native arthropod diversity evident from this study are the common exotic species, especially the Argentine ant and the European earwig. The presence of these species is not indicative — all sites have records of both species — but high numbers of either are correlated with low native arthropod diversity. For Argentine ants, this relationship is well established (Cole *et* *al.* 1992; Holway 1995; Human and Gordon 1996; Way *et al.* 1997; Holway 1998a; Kennedy 1998; Suarez *et al.* 1998; Holway 1999), but the relationship with earwigs thus far largely has been overlooked (Bolger *et al.* in press).

To find those species whose presence indicates a healthy native arthropod community, available research suggests consideration of the predator guild. Several studies have found predator numbers depressed in restorations (Williams 1993; Jansen 1997; Peters 1997), and predators are generally more sensitive to habitat area and quality. However, the sensitivity of predators to habitat quality is not likely found among all predators, but rather among those species that are largest — the "megafauna" of the arthropod realm — have limited dispersal ability, and are long-lived.

Results from this study illustrate the differential response of species within the predator guild to disturbed habitats and restorations. Mygalomorph spiders of the family Ctenizidae were found in relatively high abundance at several reference sites and one mildly disturbed site (Malaga Canyon) in the study. A single individual was found from a restoration site. These species have modest dispersal ability, mature slowly, are largely sedentary, and build trap-door nests in the soil. These features make them good indicators of a rich native arthropod fauna. An Australian study found lower abundance of mygalomorph spiders in highly disturbed remnant woodlands (Abensperg-Traun *et al.* 1996). In contrast, predaceous lycosid spiders have high dispersal ability and do not build nests. They were equally abundant in reference and disturbed sites, and superabundant at the Ocean Trails restoration site. Bolger *et al*. (in press) reported high abundance of some spider species in small, long-isolated habitat fragments in San Diego. While not identified to family level, the abundant spiders were likely lycosids.

Interactions among predators also influence predator response to habitat conditions. Polis and others (Polis and McCormick 1986; Polis and Hurd 1995) have shown intraguild predation on spiders by scorpions to be a limiting factor on spider abundance. In experiments with the artificial removal of scorpions, spider densities increased dramatically (Polis and McCormick 1986). The presence of scorpions emerges as an important factor regulating arthropod community structure in dry environments such as southern California. Bolger *et al.* (in press) recorded scorpion presence but did not explore its possible role in explaining the abundance of spiders in smaller, older, and presumably scorpion-free fragments. Other forms of competitive release are possible as well. Schoener and Spiller recorded a threefold increase in orb spiders in exclosures where predatory lizards are excluded (Schoener and Spiller 1987; Spiller and Schoener 1988; Spiller and Schoener 1989; Spiller and Schoener 1990a; Spiller and Schoener 1990b). Similar ecological interactions with vertebrates may also contribute to the patterns observed in this study and by Bolger *et al.* (in press).

Scorpions are long-lived, sedentary, and predaceous and can serve as indicators species. In the samples from the Palos Verdes Peninsula, two species were identified, one large species that constructs burrows (*Anuroctonus phaiodactylus*) and a smaller, flatter species (*Paruroctonus sylvestrii*) that lives in depressions under rocks (Hogue 1993). A few specimens of a third scorpion, probably *Vejovis* sp., were recorded. The larger species was only found at reference sites, the smaller species was represented by individuals at restored and disturbed sites, but at an order of magnitude lower abundance. These results, and the ecological significance of scorpions as regulators of other predator species as well as top arthropod consumers, make them a good indicator of arthropod community development on restorations in coastal sage scrub. This is consistent with Abensperg-Traun's findings of significantly lower scorpion densities in highly disturbed fragment woodlands (Abensperg-Traun *et al.* 1996).

The predator guild as a whole is unlikely to provide a good indication of native arthropod community status because of the different responses to environmental conditions within the guild. However, some predators, such as mygalomorph spiders and scorpions, do seem to be good indicators of a diverse native arthropod community and overall habitat quality. Surveys targeted to capture these species based on their seasonal patterns of abundance could be used to quickly assess the status of a habitat.

Variation, Monitoring, and Invasion

The fourth major theme emerging from my study of arthropods in restored and reference coastal sage scrub sites is the importance of variation in arthropod abundance, its relation to climate, and its implications for both the practical matter of effective monitoring and as an explanatory factor for the success of invasive species. The results provide insight into the seasonal character of arthropod abundance and diversity in a Mediterranean climate, the effect of such short-term climate anomalies as El Niño/Southern Oscillation (ENSO) events, and potential explanations for the indirect effects of invasive species on overall native arthropod diversity.

Yearly variation in arthropod abundance in response to physical conditions is well established and indeed is one of the reasons that arthropods are chosen as bioindicators (Kremen *et al.* 1993). The significant response of arthropods to ENSO events is likewise documented (Brantley 1995; Adis and Latif 1996; Brantley 1997; Polis *et al.* 1997). The broad taxonomic scope of this study showed that great variability exists both within and among families in their response to climatic variables. While many species show an increased abundance in response to increased precipitation — perhaps at a lag of a few months — others show decreased abundance following high precipitation. The patterns of seasonal variation probably reflect both annual reproductive cycles and differential activity levels influencing trapping results. The yearly and seasonal patterns of abundance lead to two observations.

First, although species diversity is at a maximum following the winter rains, different species exhibit their maximum abundance during all parts of the year. This means that the arthropod community is constantly changing over the course of a year. As one species is becoming more abundant, another is decreasing. This may or may not be the result of past competition resulting a seasonal partitioning of resources or it may reflect the geographic history of the species. No period of extreme cold prohibits, or greatly reduces, arthropod activity as occurs at higher latitudes, but sufficient seasonal variation exists to allow seasonal specialization. Even species within a single family express considerable variability in seasonal abundance, as illustrated by tenebrionid beetles in Chapter 2.

The seasonally dynamic nature of the arthropod community is important for designing monitoring programs. For example, if scorpions are chosen as a target for monitoring efforts, then sampling must be conducted during the summer. For ctenizid spiders, only winter trapping will be successful, consistent with results from elsewhere in the world (Baker 1986). Documentation of these seasonal patterns will also aid in interpretation of studies that present “snapshots” of the community at a few short periods during the year (Bolger *et al.* in press).

Second, a feature of the seasonal and yearly patterns of abundance of native and exotic arthropods provides an additional explanation of the success of exotic invasions. Whereas both native and exotic arthropod species show significant correlation with both precipitation and temperature time series, all native species but a few common beetles are absent from pitfall samples for some period of the year. Exotic species are found in coastal sage habitats throughout the year at much more stable levels.

This is also shown by the coefficient of variation for yearly average catch of native and exotic species. In undisturbed habitats, two exotic species exhibit the lowest variation in abundance between years — Argentine ants (CV=0.24) and European earwigs (CV=0.19). Native species show greater yearly variation in abundance and decline to zero during part of the year. One exception is the native sand roach (*Arenivaga* sp.), which was almost equally abundant every summer (CV=0.18) regardless of precipitation.

The differential responses between native and exotic species further illustrate the characteristics that make successful invaders. If exotic species are able to thrive regardless of yearly precipitation, they will have an inherent advantage over species that are more closely tied to the erratic climate. The constant abundance of exotic species also provides an opportunity for year-round interference competition, in which aggressive dominance is used to deny other species access to resources (Brown and Lomolino 1998). The exotic ants, earwigs, and sowbugs could reduce food resources for other native species at critical periods in their development. Because the current study did not address food sources and their relative exploitation by native and exotic species, this mechanism of exclusion is conjectural. However, the effects of the patterns of yearly and seasonal abundance relative to short-term climate events could be the subject of productive research.

The Plant-Terrestrial Arthropod Disconnect

The final theme to emerge from this study is the importance of the observed disconnection between vegetation characteristics and terrestrial arthropod communities at restoration sites. This lack of relationship between plant and arthropod variables is in contrast to that found at reference and disturbed sites in the study.

Results for reference and disturbed sites showed that arthropod diversity increased with native species richness and the amount of structural complexity at low levels (40–60 cm above ground), while decreasing with overall increased height of vegetation. On the theoretical side, this is consistent with the intermediate disturbance hypothesis (Loucks 1970; Connell 1978). Terrestrial arthropod diversity is highest in maturing coastal sage scrub with high plant taxonomic and structural diversity, but those sites with taller vegetation, usually correlated with less structure near the ground, begin to show decreased arthropod diversity. This situation, exhibited among reference sites at Klondike and Kelvin canyons, is the result of large individuals of *Rhus integrifolia*, which are observed to dominate coastal sage scrub on the Palos Verdes Peninsula in the absence of fire. Thus, the finding that arthropod diversity is highest at intermediate heights suggests that maximum diversity is maintained through a fire regime that keeps late succession plant species from dominating.

Restoration sites exhibit only one of the features of the relationship between vegetation and arthropod characteristics found at reference sites: terrestrial arthropod diversity decreases with increasing height at restorations. The similarity ends there. Arthropod diversity at restoration sites decreased with increasing cover of native plant species and decreased with increasing plant structure at 40–60 cm, both opposite of the relationship found for reference and disturbed sites. Furthermore, in cluster analysis using both abundance and incidence of plants and terrestrial arthropods, restored sites that clustered with reference sites based on vegetation were separated at the first division based on arthropods. For restoration sites, vegetation composition and structure does not correspond to the same arthropod community as for other coastal sage scrub sites. Several explanations for this disconnection have been discussed above, but the bottom line for restorationists and regulators is that recovery of a vegetation community that emulates reference conditions is not sufficient to ensure that a fully functioning and diverse natural community has been created.

Methods for Enhancing Native Terrestrial Arthropod Communities

The failure of terrestrial arthropods in restorations to track vegetation characteristics presents a difficult problem for regulators and restorationists. It means that even a complete revegetation, successful by all vegetation parameters, does not necessarily support a native terrestrial arthropod community. I have argued elsewhere that creation of a complete, historically accurate plant community is a necessary part of restoration (Longcore *et al.* 1999), but it is not sufficient to ensure recovery of the vertebrate and invertebrate community. Unfortunately, no easy solutions exist to solve the problem. The suggestions included herein provide rough guidelines to maximize the continuity of remnant native arthropod communities. However, further research is necessary to identify methods to enhance native arthropod communities. These methods are likely to depend on the specific ecological parameters of identified native arthropods and may involve active reintroduction, microhabitat creation, or exotic species control.

Reintroduction of invertebrate species in restoration efforts has thus far largely been limited to butterflies (Samways 1990a). As research into butterfly reintroductions shows, understanding each species' autecology is critical to the success of the project (*e.g.*, Davis 1989). Attempted butterfly reintroductions have met with mixed success (Samways 1990a; Williams 1995; Webb and Pullin 1996; Marttila *et al.* 1997; Wynhoff 1998). For other invertebrates, Bowler (1993) has suggested reintroduction of trap-door spiders from areas threatened by development, but such efforts have not yet been documented. Future reintroduction attempts will require identification of those species missing in restoration arthropod faunas, investigation of the habitat requirements of those species, creation of such habitat features that are missing, identification of source populations, propagule capture, reintroduction, and monitoring. With hundreds of arthropod species native to coastal sage scrub — others have identified 185 spider species alone (Prentice *et al.* 1998)

— the research effort that would be required to reassemble an arthropod community through reintroduction would be overwhelming.

Reintroduction would be used to rectify the inability of arthropod species to overcome dispersal barriers that inhibit colonization of a restoration site. It is possible that many arthropods are able to disperse to restoration sites but do not have suitable habitat. Addressing this possibility will also require extensive autecological research on many species. The microhabitats at restoration sites may not be sufficient for native arthropods in many ways: compacted soil, too much organic matter, lack of soil fungi, no dead wood, etc. Identification and correction of these deficiencies will require a similarly large research and implementation effort.

Finally, actively attempting to recreate a terrestrial arthropod community would surely include efforts to control the abundance of exotic species. Argentine ants are the most studied invaders and there is some indication that limiting the water available at a site will decrease their abundance. I have observed Argentine ants invade a site under irrigation, driving out harvester ants, and then seen the Argentine ants retreat and the harvester ants rebound when the irrigation was removed. This observation would need to be substantiated by direct research, but it does lead to a suggestion that irrigation be removed from restoration sites as soon as possible. Little is known to formulate recommendations for the control of other exotic species as part of a restoration effort.

Conclusion

The disturbing reality is that restoration projects completed as compensatory mitigation are not recreating the natural communities that they were intended to replicate. Although progress continues to be made in restoration design and implementation, the goal of actually returning a system to its state prior to human disturbance remains a distant one. Therefore, the most important recommendation that stems from this research is that the use of restoration as compensatory mitigation be avoided as much as possible. There is much greater conservation value in paying to protect undisturbed or slightly disturbed habitats than in trying to recreate those habitats elsewhere. Where destruction of native habitats must be permitted, restoration attempted as mitigation should always be at a multiple larger than the impacted area to make up for the decreased natural values inherent in restorations versus native habitats. Aggressive mitigation ratios should be adopted as a matter of policy to discourage the use of restoration in favor of avoidance as a mitigation tool.

A realization of the shortcomings of restoration should also be included in regional habitat planning exercises such as the NCCP. These multispecies conservation efforts plan for the loss of habitat in one area and make up for it through restoration elsewhere (California Department of Fish and Game 1999). The results of this study and others on arthropods in restoration caution against this approach particularly if conservation of biodiversity is the program goal.

Restoration and other forms of active management are important to the preservation of biodiversity in a world dominated by human action. However, we should set aside the hubris that allows us to think that we can recreate natural habitats. As restorationists, we should observe the Hippocratic Oath and “do no harm” — working to preserve even the smallest components of the ecosystem. As planners, we should reduce our reliance on the technological fix of restoration and work harder for preservation.

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